THE UNIVERSITY OF ALBERTA

THE ECOLOGY OF HIPPOPOTAMI (*Hippopotamus amphibius*) IN SOUTHWESTERN KENYA

by

© ELSEN LARS KARSTAD

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

WILDLIFE PRODUCTIVITY AND MANAGEMENT

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

SPRING, 1984

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR ELSEN LARS KARSTAD

TITLE OF THESIS THE ECOLOGY OF HIPPOPOTAMI (*Hippopotamus amphibius*) IN SOUTHWESTERN KENYA

DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED SPRING, 1984

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) E. Karstad

PERMANENT ADDRESS:

Dept. Animal Science
U. of A., Edmonton
Alberta, Canada
T6P 2E3

DATED MAR. 01 1984

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE ECOLOGY OF HIPPOPOTAMI (*Hippopotamus amphibius*) IN SOUTHWESTERN KENYA submitted by ELSEN LARS KARSTAD in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

.....

Supervisor

.....John S. Stelfox...

.....

.....

Date..March 01.....1984

ABSTRACT

This study was conducted in response to concern over the impact of hippopotami upon the riverine habitat of the Mara River in Narok District, Kenya. Between 1960 and 1982, the yearly increase of hippopotami along 128 km of river averaged 12%. In 1982, the population consisted of over 2800 animals. Between 1980 and 1982, a change in animal distribution led to increased densities (6.8 to 19.8 per km of river) within areas previously supporting low animal numbers to the north of the Masai Mara National Reserve. Within the reserve, animal numbers remained largely unaltered, a marginal increase of 0.07 per km of river for the same period.

The distribution of hippopotami along the river was determined primarily by river morphometrics. Little evidence of spatial selection was apparent for adjacent upland habitat type. Day-habitat limitations within the river were investigated by examining both seasonal fluctuations in animal distributions and social responses to changes in group composition.

Crowding within pools resulted in significant increases in persistent aggression, though few serious fights were observed. As the availability of suitable pools decreased with lower water levels, hippopotamus densities within the remaining pools increased. From 29 to 171 animals occupied the major pool within the study section. Aggression appeared associated with densities within pools, mainly due to the

territorial behaviour of dominant males.

Vocal, olfactory, auditory and visual means of communication were identified. Dominant and submissive roles were clearly identified through ritualized defecations. The maintenance of territories by dominant males was confirmed. Resultant spatial distribution along the river limited access to pools for a section of the population, primarily bachelor males.

Monthly phytomass of herbaceous vegetation within the foraging radius of hippopotami ranged from 205 to 1160 kg/ha. Partitioning resources on a seasonal and spatial basis amongst the major herbivore species indicated that hippopotami were susceptable to rainfall-mediated forage constraints. Hippopotami experienced forage availability restrictions during the driest months, when daily intakes were estimated to be only 75% of daily intake requirements.

The impact of hippopotami upon the riparian environment was assessed. Extensive riverbank degredation was caused by the establishment and use of entrance/exit paths and mineral digs into riverbanks. An average of 24 m^3 of soil per km of river per year was eroded from the riverbank from the inland progression of hippopotamus paths. The impact on range vegetation was minor, although the massive nutrient drain from the range to the river via feces must have long term effects.

Human/hippopotami conflicts were not serious during the study. Some crop depredation by hippopotami upon small

vegetable plots was reported in the northern part of the study area. However, land use changes in the Mara will result in an increase in land devoted to crop production and more frequent conflict between people and hippopotami.

ACKNOWLEDGEMENTS

I am grateful to the Kenya Range Ecology Monitoring Unit (KREMU) for providing support including aircraft for the two initial aerial counts. Mr. J. Ole Naiguran, Senior Warden, assisted in providing permission and a ranger for streamside counts within the Reserve. Thanks also go to Mr. J. Dawson and Mr. C. Sandmeyer, who provided moral and logistical support in the field, and Dr. J Stelfox, who arranged the 1980 flights. The continuous support and encouragement of KREMU's project manager, Mr. D. Andere is gratefully acknowledged. Funds were provided by C.I.D.A., the African Fund for Endangered Wildlife, the University of Alberta, and my father, Dr. L. Karstad. Mr. R. Weingardt and Mr. G. Godby assisted in the statistical analysis. The support and advice of my academic committee members, Dr. W. Samuel, Dr. J. Stelfox, and Dr. J. Kennelly are appreciated. Dr. H. Klingel provided some valuable insights into the behaviour of hippopotami during a two-day stay at my field camp, and provided the telephoto camera lenses used in the study. Dr. A. Sinclair provided a critical review of Chapter 2.

To the many people who have aided in the fieldwork I give my heartfelt thanks, particularly to B. Lewis for her assistance during the first month of confusion (including one robbery). I am indebted to my advisor, Dr. R. Hudson. His insight, motivation, and energy has been a constant inspiration.

This thesis is dedicated to my father, L. Karstad, who throughout my life has instilled in me an appreciation of wildlife, as well as the motivation and opportunity to conduct this study.

Table of Contents

Chapter — Page

I. GENERAL INTRODUCTION 1

Dynamics of the Mara-Serengeti Ecosystem 2

Environment 2

Animal Populations 4

Study Objectives 6

II. CENSUS OF THE MARA RIVER HIPPOPOTAMUS POPULATION .. 10

Introduction 10

Methods 10

Results 14

Calibration of Aircraft 14

Total Counts and Rate of Increase 16

Distributions 18

Grouping 20

Discussion 20

Counting Methodology 20

Populations and Distributions 26

III. HABITAT ASSOCIATIONS 30

Introduction 30

Methods 31

Analysis of Terrestrial Habitat 31

Analysis of Aquatic Habitat 32

Results 33

Land 33

River 34

Discussion 40

IV. SOCIAL ORGANISATION AND COMMUNICATION 44
Introduction 44
Methods 46
Group Composition 46
Individual Identification 48
Behavioural Observations 48
Water Levels 50
Statistical Analysis 51
Results and Discussion 52
Group Stability and Movement 52
Agonistic Behaviour 56
Communication 61
Visual Signals 62
Vocalization 67
Defecation 69
Summary and Conclusions 72
V. FORAGE RESOURCE LIMITATIONS 75
Introduction 75
Methods 77
Seasonal Biomass Measurements 79
Distribution of Grazed Areas 79
Herbivore Census 80
Statistical Analysis 81
Results and Discussion 82
Seasonal Grass Biomass 82
Distribution of Grazed Areas 85
Ungulate Populations 88

Rangeland Productivity and Offtakes 91

VI. ENVIRONMENTAL IMPACTS 101

Introduction 101

Methods 104

Range Condition 104

Seasonal Dynamics of Grazing Mosaics 104

Riverbank Degradation 105

Results and Discussion 105

Seasonal Dynamics of Grazing Mosaics 105

Bare Earth and Litter Within the Grazing Mosaic 108

Fire Exclusion and Woody Vegetation Regeneration 110

Riverbank Degradation 111

Human/Hippopotamus Interactions 113

VII. SUMMARY AND CONCLUSIONS 117

Population Status 118

Population Limitations 120

Environmental Impacts 123

LITERATURE CITED 126

APPENDICES 132

River Current and Width Measurements 132

Recorded Mortalities and the Ages of Collected Skulls 137

Estimating Herbage Biomass by the Horizontal Intercept Method. 141

Ungulate Census, Sept./81 - Oct./82. 149

Masai Questionaire 164

List of Tables

Table		Page
II.1	Aerial and ground surveys of hippopotami within the Mara River, including correction factors	15
II.2	Aerial surveys, 1982. Flight one; Sept. 18, flight two Oct. 1	16
II.3	The 1980 and 1982 censuses of hippopotami on the Mara River	25
III.1	KREMU Habitat Classes (Epp and Agatsiva 1980) found adjacent to 124 km of the Mara River	34
III.2	Recorded morphometrics of a 10 km stretch of the Mara River	40
IV.1	Agonistic encounters observed over 112 hours of observation (1630 to 1830 hrs)	60
V.1	Average individual body weights per species included in weekly census	81
VII.1	Recorded densities of hippopotami per Km of river	118
VII.2	Available grazing area per hippopotamus, as recorded for various populations	120

List of Figures

Figure		Page
II.1	The study area	11
II.2	Densities of hippopotami observed per km of river by sector, 1980	17
II.3	Density of hippopotami by sector for 1980 and 1982 censuses	19
II.4	Frequency distribution of group sizes over the 124 km study section	21
II.5	Increase of hippopotami within the Mara River inside the Masai Mara National Reserve, 1959 - 1982	28
III.1	Major habitat types along 124 km of the Mara River	37
III.2	Main Pool schematic, showing exit/entrance paths and group areas	38
III.3	Occupancy of Main Pool by hippopotami, as influenced by water levels in the Mara River	39
IV.1	Typical head morphologies for (A) adult males, and (B) adult females (sketched from photos)	47
IV.2	Example of an individual identification photograph	49
IV.3	The monthly distribution of group 1 over three pool locations	55
IV.4	Hippopotamus numbers per month within the 10 km study section	57
IV.5	Percentage of aggressive encounters initiated by sex/age class	59
IV.6	The probability of dominant male gape, expressed as percent per 30 minute period	65
IV.7	The probability of gape for all individuals, expressed as percent per 30 minute period	66
IV.8	The average number of vocalizations within groups per 30 minute period	68

Figure		Page
V.1	Average monthly herbaceous biomass (kg/ha) estimated from riverine plots, September 1982 - November 1982	83
V.2	Percent of range grazed during 1981 and 1982 long-grass seasons	86
V.3	Average monthly ungulate biomass by catena, from July 1981 to September 1982	90
V.4	Monthly precipitation records for Buffalo Camp, from July 1981 to October 1982	92
V.5	Estimated grassland offtakes by censused ungulates, from July 1981 to September 1982	93
V.6	Estimated monthly forage removals by Wildebeest for all catenas, from July 1981 to September 1982	94
V.7	Estimated monthly forage removals by Zebra for all catenas, from July 1981 to September 1982	95
VI.1	Hippopotamus grazing mosaic locations within two transects measured during long-grass conditions, 1981 and 1982	106

GENERAL INTRODUCTION

The rangelands of the Mara-Narok area, north of the Serengeti National Park in Tanzania, support the highest densities of herbivores in Kenya (Andere 1980). Conditions have remained largely unaltered for at least a million years (Sinclair and Norton-Griffiths 1979) allowing for the formation of a complex grazing system dominated by large herbivores.

Today, the Mara-Serengeti ecosystem is recognized as one of the last truly great wildlife spectacles in the world. Tourism has been the major economic incentive for the establishment and maintenance of the Masai Mara National Reserve in Kenya and the Serengeti National Park in Tanzania. The greatest attraction is the annual migration of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) between wet season range in Tanzania and the dry season range in Kenya. A great variety of species comprises the mammalian community, including a striking diversity of herbivores. It is not uncommon to see 8 or 10 species at one time sharing the same grazing area.

Pratt and Gwynne (1977) describe most of the rangelands in East Africa as having low or erratic rainfall, destined to remain as rangelands because of their poor potential for agriculture or other development. An altered rainfall regime and socio-political changes in the Mara-Narok area have opened this region to large and small scale farming. Increased human settlement on the periphery of the protected

areas has restricted the range available to wildlife in the west and north of the Mara-Serengeti ecosystem. A system of group ranches allocated to the traditionally nomadic Masai pastoralists during the 1970's has introduced the concept of land ownership. Further subdivision of group ranches into individual holdings is planned. A direct consequence is the now common practice of leasing tracts of land to outside farm operators. Both large and small scale farms have been established throughout the Mara-Narok area, with new interest being generated by recent successful harvests. These changes have led to an urgent demand for definitive wildlife research and management. Conflicts between wildlife and agriculture are on the increase, and will continue to do so. At the same time, the cultural and economic values of wildlife are becoming more apparent.

Dynamics of the Mara-Serengeti Ecosystem

Environment

The most important environmental factor in the Mara-Serengeti region is rainfall. Patterns are large scale and influenced by topography. The major weather pattern in East Africa is established by the Intertropical Convergence Zone (Sinclair and Norton-Griffiths 1979). Precipitation patterns for the Mara-Serengeti region are bimodal, with the majority of rain being delivered from November to May.

According to Pratt and Gwynne's (1978) eco-climate classification, the study area is within zone IV, dominated by a *Themeda-Acacia* association. The rangeland is described as wooded grassland dominated by the grasses *Themeda triandra*, *Pennisetum mezianum*, and *Digitaria milanjiana* and several tree species of the *Acacia* and *Commiphora* genera. The rangelands of the Mara-Serengeti are considered to be amongst the most productive in East Africa.

The rangelands of the Mara-Narok area in southwestern Kenya are drained primarily by seasonal watercourses. The major permanent river is the Mara River, flowing southwestern from headwaters in the Loita hills and the Mau Range. It continues south-southwest along the Siria escarpment as far as the Northern perimeter of the Masai-Mara Game Reserve. From the Reserve boundary, the river meanders south to the Tanzania border and eventually flows in a south-westerly direction to Lake Victoria. The three main tributaries of the Mara River, all seasonal, are the Oltotua River from the northern Loita plains, the Talek River from the central Loita plains, and the Sand River originating from the Loita Hills (Epp and Agatsiva 1980). Numerous washes, dry during all but the wet season, feed into the Mara River and it's major tributaries. These channels are important to surface drainage and provide microhabitats utilized by many wildlife species.

Animal Populations

Rinderpest was introduced into East Africa in the late 1800's. The effects of the massive initial epizootics killed 95 percent of the cattle and and a large portion of the wildlife (Sinclair 1977). Though the reservoir for the virus was within domestic cattle populations, wildebeest and buffalo populations were severely affected, often on an annual basis, until a generalized cattle vaccination program was instituted in the late 1950's. From 1963 to 1977 no reinfections were noted among either wild or domestic animals (Sinclair and Norton-Griffiths 1979). Of late, evidence of the virus' reestablishment within the buffalo population in the Serengeti has been collected (L. Karstad, Veterinary Research Laboratories, Kabete, pers. comm.).

Beginning in 1969, a more equitable distribution of rainfall has resulted in increased grassland productivity (Sinclair 1977, Sinclair and Norton-Griffiths 1979). Total rainfall has not increased; dry seasons have become less severe, allowing a perennial grass response ('greenflush') periodically throughout the driest months. In addition, the effective growing season for annual grasses has been extended.

Initially responsive to the elimination of rinderpest and subsequently responding to increased forage supply, most large herbivore populations have increased substantially within the Mara-Serengeti ecosystem (Sinclair and Norton-Griffiths 1979). Symptomatic of ecologic

perturbations is the rapid expansion of populations such as has occurred most noticeably within the buffalo, wildebeest and hippopotamus populations in the region. Such dramatic population expansions are also common to animal and plant species introduced into ecosystems as exotics, and result from a superabundance of food.

Hippopotami are apparently not fatally susceptable to rinderpest (Plowright *et al.* 1964). Still, indirect stimuli resulting from the elimination of the disease may have been felt, as hippopotami rely on short-grass grazing during the long-grass season and share grazing resources with other species. The availability of suitable grazing areas increases proportionally as the long-grass is reduced by grazing, providing more extensive swards of short-grass during the long-grass season. Without high densities of herbivores, the long-grass would dominate and provide fuel for extensive range fires.

During the initial period of population increase following rinderpest control, the dry seasons were 'normal', allowing little if any grass growth during the dry season (Sinclair and Norton-Griffiths 1979). The expanding hippopotamus population apparently did not reach a size that would have imposed forage limitations upon further growth before 1969, the beginning of the present moist rainfall regime.

Surveys of the plains game within the Mara-Narok region have been conducted over the past five years, primarily by

the Kenya Range Ecology Monitoring Unit (KREMU). Because of the riparian distribution of hippopotami within the Mara River, little information has been collected concerning population size and rates of increase prior to this study.

Study Objectives

In spite of the ability of hippopotami to dramatically alter riparian and lacustrine habitats (Bere 1959, Lock 1972), very little information has been collected pertaining to their ecology and role in ecosystem dynamics. Ethological investigations have been undertaken, notably Klingel (1979), though dealing primarily with lake-dwelling hippopotami. The bulk of published literature comes from one population resident within the Kazinga Channel area, Uganda, that was subject to a massive reduction scheme during the 1960's.

Whether this paucity of information stems from a general lack of scientific interest in this species, or the possibility that populations are only rarely in a state of disequilibrium, is not known. Possibly the restricted demographic distribution of hippopotamus populations, being dependent on permanent water sources, has led ecologists to disregard it's role in ecosystems. Hippopotami of the Mara River are not mentioned in Sinclair and Norton-Griffiths (1979) text on the dynamics of the Serengeti ecosystem.

This study was initiated in response to concern over the potential deleterious impact of hippopotami within the Mara River, in light of the population's rapid growth. In

1979, a cursory aerial survey of the Mara River within the Masai Mara National Reserve revealed a surprisingly large population of hippopotami (Mwenge International Associates Ltd. 1980). As hippopotami had previously established a reputation for rapid and sustained population growths, and resultant dramatic habitat modification (Spinage 1958, Pienaar *et al.* 1966), concern was expressed with regard to the potential for similar impacts along the Mara River.

The basic areas of inquiry, essential to the formulation of management plans for this population, include the following:

1) What is the current status of the population, and is there evidence of intrinsic regulation which will stabilize the population without intervention?
2) If regulation of the population is evident, is it responsive to social or resource-based limitation?
3) Is the population already so high that the soils, flora, and fauna within its habitat are already adversely affected?
4) Have conflicts with human enterprise become serious enough to impliment control programmes?

These questions were addressed through a field investigation designed to identify the mechanisms of population regulation, and the existing and projected impact of hippopotami within the Mara River habitat. Like most field studies on large mammals, the approach was, of necessity, descriptive. There were few opportunities for

experimental manipulation of such a large and dangerous animal in a two year study. However, seasonal cycles and annual trends, and the eruptive state of the population offered 'natural experiments' which were used as much as possible to investigate the complexities of a dynamic system in a cross-sectional study. Field studies were conducted in two parts; initial censuses were conducted during July and August 1980, and the major portion of fieldwork undertaken between April 1981 and October 1982.

This study is reported as five research papers. The first describes the current size and distribution of the population and provides evidence that the population may be beginning to stabilize. Habitat requirements of the Mara River hippopotami are investigated in the second paper, and evidence is provided that the distribution of hippopotami was determined by site selection within the Mara River, not by foraging habitat. In an attempt to determine the relative importance of resource and social limitations, the third paper evaluates the social dynamics and structure of the population and provides evidence that agonistic behaviour probably is not involved directly in population regulation. The fourth paper addresses the forage resource. Seasonal vegetative productivities and ungulate offtakes are assessed, indicating that dry season forage availability was limited to below estimated daily requirements for hippopotami resident within the Mara River. The fifth paper summarizes the overall population status in terms of

environmental impacts, focussing on range condition and trends, the hippopotamus' role in rfire ecology, riverbank degredation, and existing and potential human/hippopotami conflict.

CENSUS OF THE MARA RIVER HIPPOPOTAMUS POPULATION

Introduction

The hippopotamus is the dominant herbivore in terms of biomass for areas proximal to the Mara River, and imposes an important impact on vegetation and perhaps other wild and domestic herbivores. Hippopotamus numbers within the Mara River have increased markedly over the past two decades. Darling (1961) estimated 120 hippopotami within the Reserve in 1959, while Olivier and Laurie (1974) estimated 738 during their 1971 study. The Very Large Herbivore Study (Mwenge International Associates Ltd. 1980) estimated over 1200 animals along 75 km of river within the Reserve.

As part of this study on the impact of hippopotami on their environment, an updating of previous censuses was conducted in order to define the continuing population trend. The purpose of this census was to follow the expansion of the hippopotamus population through 1982, and to document changes in it's distribution.

Methods

Ground counts (Aug. 10-23 1980) covered the 127 km census section (Fig. II.1) with the exception of a 31 km stretch (sector B) of thick riverine forest that was considered unsafe to enter (Karstad *et al.* 1980). Enumeration of individuals within groups required considerable patience since only part of the group was at

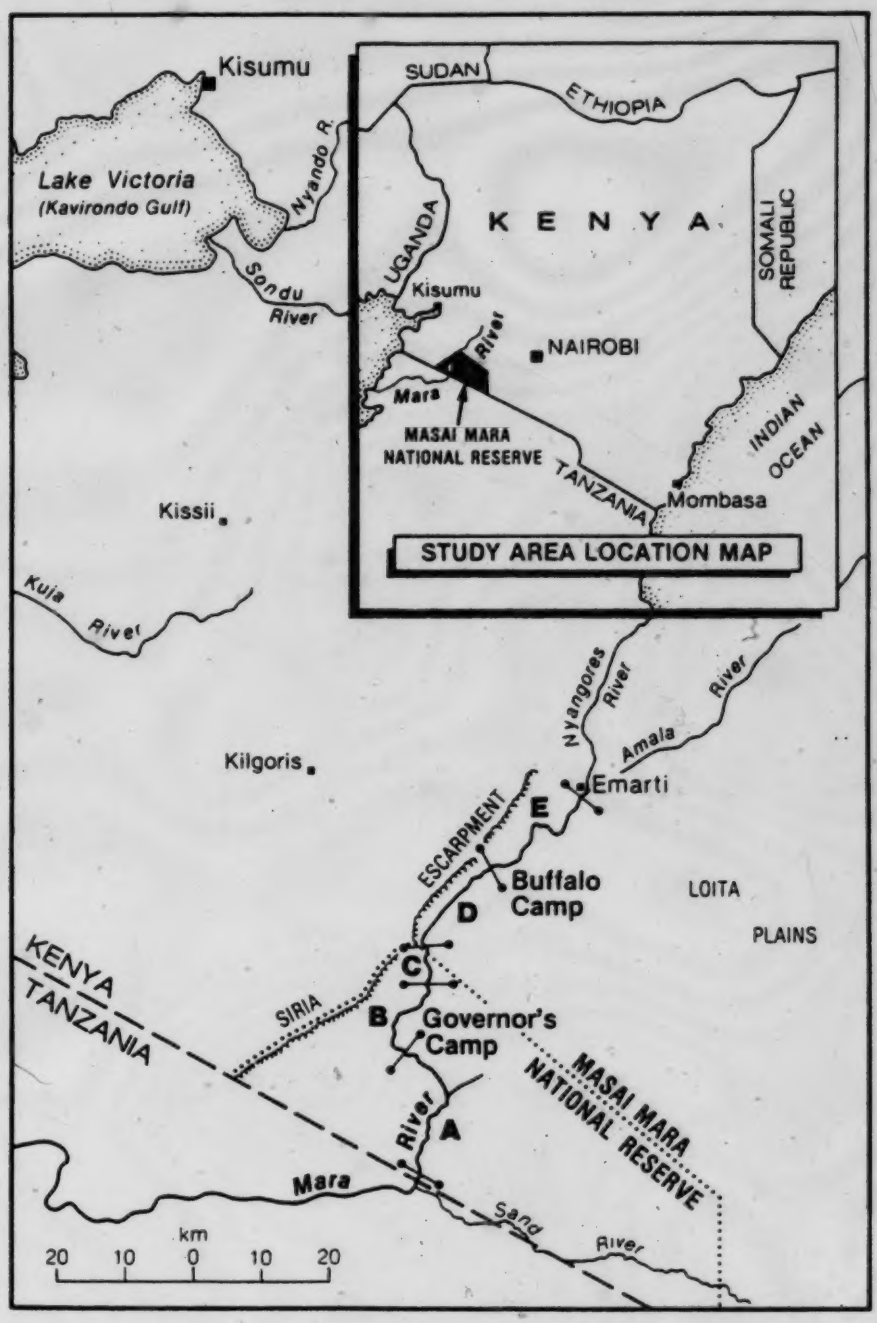

Figure II.1 The Study Area. The Mara River, sectors A through E are shown.

the surface at any one time. Use of a mirror to reflect sunlight from a position downwind of the hippopotami was useful for evoking curiosity, bringing most of the animals to the surface.

All counts were conducted along 125 km of river from the first Mara bridge near the Tanzania border to the Emarti bridge, northeast of Aitong. Flights were made approximately 100 m above ground level at an average airspeed for all aircraft of 100 kph, with the aircraft circling sharp bends in the river, when necessary to provide a clear view. Flight directions were into the wind in order to minimize equivalent ground speed. Locations and numbers of individuals within groups were identified by one or two-rear seat observers and recorded on 1:50,000 topographic maps by the front seat navigator. Counts were conducted from mid-morning to late-afternoon, the period when the maximum number of animals are within pools.

On August 9 1980, the first aerial census was conducted. Starting at 1500h using KREMU's twin-engined Partenavia, the flight was made in an upstream (north) direction. Two rear-seat observers, at each side of the aircraft, enumerated animals in and along the river.

The second flight was made on Nov. 20 1980 using a single-engined Cessna 185 in order to capitalize on slower flying speeds and greater maneuverability. The count began at 1100h and was conducted in a downstream (south) direction with two-rear seat observers and a front seat navigator.

This census and the ground count provided the bias correction factors used for the subsequent aerial surveys with similar aircraft.

The final two aerial counts were made on Sept. 17 and Oct. 1, 1982, beginning at 1030h. Identical procedure was followed and the two aircraft were similar, Cessna 180 and 182, with the door adjacent to the observer removed. One observer viewed from both sides of the aircraft, though with the exception of sharp meanders the aircraft parallelled the east side of the river with the observer at the open door. Photographs were taken of several large groups during this flight in order to determine if infrared black and white film could aid in counts by revealing submerged hippopotami. The technique did not appreciably improve visibility into the turbid water.

Aerial and ground counts were conducted as total counts, therefore the question of precision did not arise. The important consideration was bias. It was assumed that the ground counts were close to the actual numbers of animals, and bias correction factors for aerial data were calculated by dividing the ground count by the aerial count for respective census sectors.

These census sectors were delineated on the basis of access, animal density and river morphology, primarily meander. For sector B, not surveyed during the ground counts, the mean correction factor for the four sectors included in the ground count was applied in order to

estimate hippopotamus numbers. As totals within the reserve were necessary for comparison with previous counts, a sector division was placed on the northern reserve boundary.

Results

Calibration of Aircraft

The efficiency of aerial census using the Partenavia averaged 52% when compared with the ground count. In the Reserve where hippopotamus densities were over 20/km of river, the bias-correction factor was (x)2.14 for this aircraft. North of the Reserve, where densities fell to less than 10/km, the correction factor was 1.29.

Counting efficiencies for the Cessna were considerably higher (Fig. II.2). Within the Reserve corrections were 1.24, outside 2.21, for an overall correction of 1.34 (Tables II.1 and II.2). These correction factors were applied to all subsequent aerial counts in order to estimate actual numbers. This assumes that the ground census provided an unbiased estimate. Repeated counts made on foot over specific sections of river indicated that ground counts were generally accurate, and if error was made, it was invariably a slight undercount.

Total Counts and Rate of Increase

The minimum estimate (ground counts) of hippopotami for the entire census section from the Tanzania border to the

Table II.1. Number, bias correction factor, group size and density of hippopotami on the Mara River, southwestern Kenya, as determined by ground and aerial surveys. Aerial survey conducted Aug. 9 1980, ground survey conducted Aug. 10-23 1980.

Sector	Observed number of hippopotami [1]	Bias correction factor [2]	Observed Mean group size	Length of sector (km)	Corrected density (hippoptami/km)
A. Tanzania border to south of Governor's camp	(808)	-	(10.0)	38.6	(20.9)
	677	1.19	11.9		17.5
	486	1.66	7.8		12.6
B. Governor's camp forested area [3]	(888)	-	(14.0)	31.4	(28.3)
	683	-	12.2		21.8
	327	-	8.2		10.4
C. Wooded section to north border	(94)	-	(13.4)	4.2	(22.4)
	78	1.21	15.6		18.8
	25	3.76	25.0		6.0
Sub-total Mara Reserve	(1990)	-	(12.5)	74.2	(24.1)
	1438	1.24	12.2		19.4
	838	2.14	8.2		11.3
D. North Reserve border to Buffalo Camp	(189)	-	(6.5)	20.9	(9.0)
	105	1.80	8.1		5.0
	125	1.51	4.2		6.0
E. Buffalo Camp to Emarti Bridge	(153)	-	(12.8)	29.3	(5.2)
	50	3.06	7.1		1.7
	140	1.09	7.4		4.8
Sub-total outside Mara Reserve	(342)	-	(8.6)	50.2	(6.8)
	155	2.21	7.8		3.1
	265	1.29	5.1		5.3
Grand total	(2132)	-	(9.9)	124.2	17.2
	1591	1.34	11.4		12.8
	1103	1.93	7.1		8.9

[1] Results of ground survey (in parentheses) followed by results for Cessna and Partenavia, respectively.

[2] Ground count/aerial count.

[3] Sector B not ground-counted. Estimate derived from aerial count by Cessna times overall correction

Table II.2. Results of two aerial surveys of hippopotami on the Mara River, 1982 (Flight one, Sept. 18; Flight two, Oct. 1).

Sector	Observed number of hippopotami	Bias correction factor	Observed mean group size	Sector length (km)	Corrected density (hippopotami/km)
A. Tanzanian border	855	1.19	8.60	38.6	22.2
to south of	773		6.79		20.0
Governor's Camp					
B. Governor's Camp	595	1.34	11.75	31.4	18.9
forested area	595		9.02		18.9
C. Wooded section	42	1.21	7.93	4.2	10.0
to north border	52		26.0		12.4
Sub-total Mara	1492	1.24	9.81	74.2	20.1
of Reserve	1420		7.84		19.1
D. North Reserve	222	1.80	9.65	20.9	10.6
border to	249		9.58		11.9
Buffalo Camp					
E. Buffalo Camp to	180	3.06	10.11	29.3	6.1
Emarti Bridge	194		8.61		6.6
Sub-total north	402	2.21	9.80	50.2	8.0
Reserve	443		9.16		8.8
Grand total	1894	1.34	9.81	124.2	15.2
	1863		8.10		15.0

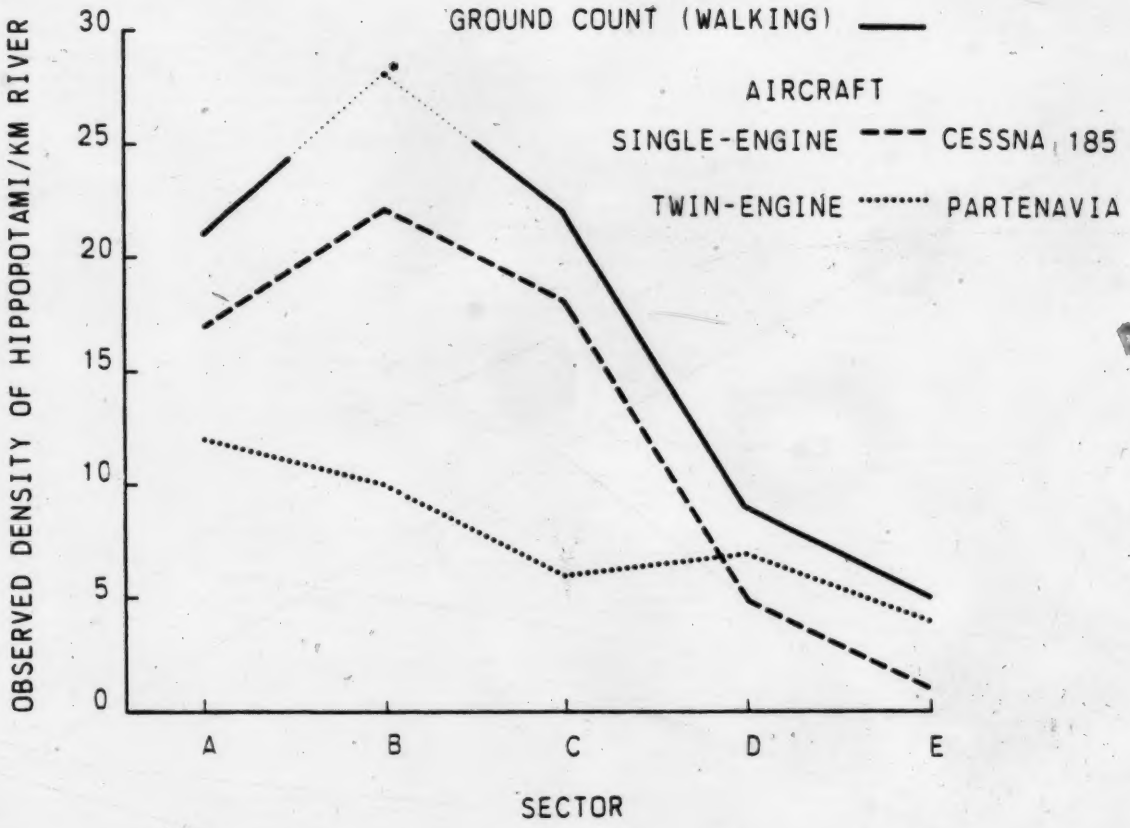

Figure II.2 Densities of hippopotami on the Mara River as determined by two aircraft types and a ground count. The Partenavia was used on Aug. 9, the Cessna on Nov. 20, 1980. Sector B was not walked; the estimate (*) was derived by applying the Cessna bias correction averaged from sectors A, C, D and E.

Emarti bridge, in 1980, was 2132. This number included an estimate derived from the aerial counts for the one 31 km sector (sector B), not walked (see Fig. II.2). Two years later, in 1982, corrected results from two aerial surveys provided an averaged estimate of 2819 (Table II.1). This represented a 24.4% increase over the 1980 census, an intrinsic annual growth rate of 15%. Most of this increase had occurred outside the Reserve; 70.5% annually within sectors D and E between 1980 and 1982 (Fig. II.3). The difference in animal numbers inside and outside the Reserve was highly significant between the 1980 and 1982 counts ($Chi^2=229$, $p<0.001$). Raw data from Cessna flights indicate an annual increase of 8.5% between 1980 and 1982. As the major influence on count accuracy from aircraft was the relative meander of the river, and considering density redistributions occurred into sections of river with high meander, bias-corrected estimates were more representative.

Distributions

Density distribution of hippopotami along the five sectors of the Mara River differed between 1980 and 1982 (Fig. II.3). Overall, the densities within the Reserve remained the same between the two counts while outside the Reserve densities increased from 6.8 to 19.8/km (Table II.1).

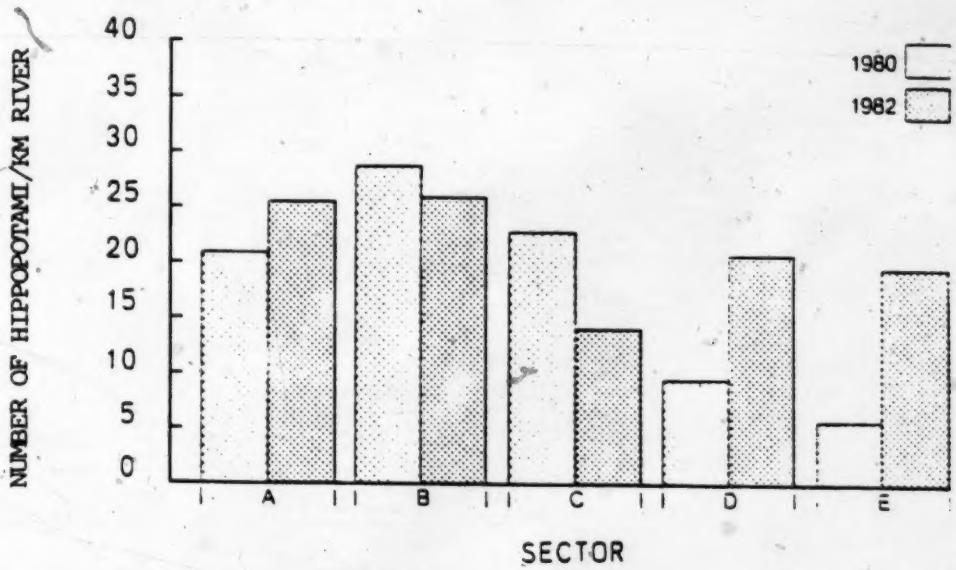

Figure II.3 Density of hippopotami in the Mara River study area for 1980 and 1982. Ground count data are used for 1980; corrected aerial data for 1982.

Grouping

Average group sizes for the 1980 and 1982 counts were 10.6 and 8.9, respectively. A higher proportion of groups with 5-10 individuals, as well as large aggregates of 40 or more, were noted in 1980 (Fig. II.4). Group sizes exhibited different modal frequencies between 1980 and 1982; 5-10 and 2-5 respectively. Water levels were considerably lower during the counting period in 1980, resulting in fewer groups and a higher proportion of the population within large groups.

Discussion

Counting Methodology

Census methods for hippopotami are not as highly standardized as they are for plains game. Several methods have been used, including streamside and boat counts (Ansell 1965, Attwell 1963, Olivier and Laurie 1974, Pienaar *et al.* 1966, Villijoen 1980). For monitoring large areas, aerial counts have obvious advantages if corrections for counting bias can be applied. Olivier and Laurie (1974) provided the first systematic attempt to derive correction factors. They determined a factor of 1.15 for hippopotami partially submerged in shallow water and 2.65 for hippopotami in deep water, based on counts with a Piper Super Cub.

For this project, empirically-derived correction factors were selected, as the major influence on counting

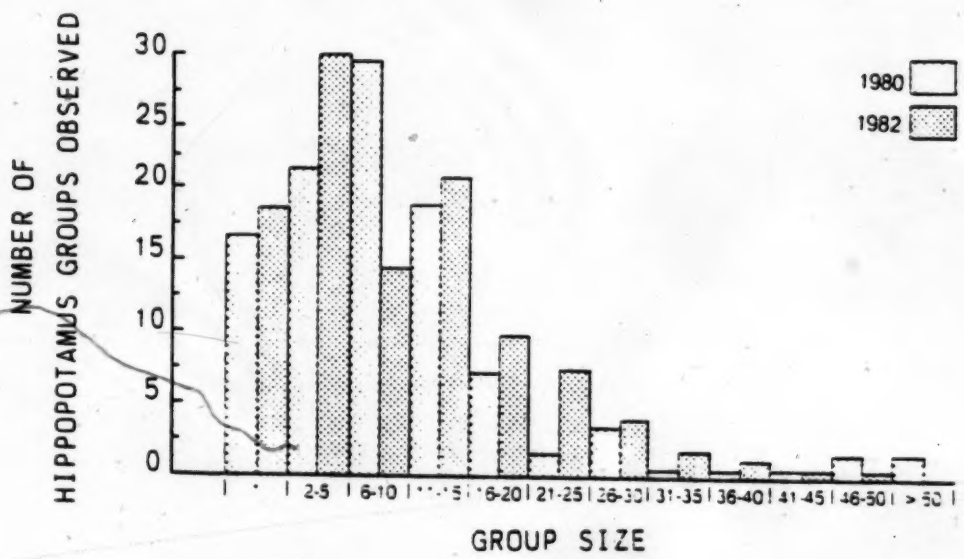

Figure II.4 Frequency distribution of hippopotami group sizes over the 124 km study section of the Mara River. Ground count data are used for 1980; corrected aerial data for 1982.

accuracy appeared to be the relative meander of the river, as a convoluted rivercourse required tight maneouvering in order observe the sharp bends of the river most frequented by hippopotami. Allowance was made for varied river morphology by applying individually derived correction factors to each of the five sectors. Olivier and Laurie's (1974) method of applying bias-corrections based on immersion depths recorded for each animal spotted, was not employed, This departure from a previously established technique was justified by the much larger population, necessitating quicker group counts over shorter periods.

Aircraft maneouverability is of primary importance in counting efficiency. Sharp meanders and stretches of high forest canopy bordering the river require the river course to be followed closely. Error from missing entire groups is increased if repeated circling is needed. Circling was avoided if possible, large groups were counted only once without circling, providing a clear view of the entire pool was available. Much more circling was necessary with the large Partenavia, compared to the Cessna flights, resulting in higher bias correction factors. Navigational error, when it occurred, was localized. Several prominent landmarks were used as guides, and sector divisions were easily recognized. Airsickness, resulting from frequent tight turns occurred on all but the last flight, affecting both observers and navigator.

Flying speed is considered of secondary importance. A low altitude is necessary in order to distinguish hippopotami from rocks. Thus, the observer must make quick and accurate counts, often over pools with 40 or more animals. The three aerial counts with Cessna aircraft following the Partenavia survey all had comparable minimum flying speeds of approximately 100 kph. The formulation of correction factors is based on one flight for each of the two different aircraft types, single and twin-engined. Thus, a bias occurring in either the foot census or the initial flights will be reflected in all subsequent census efforts through the bias-correction factors for either of the two aircraft types. Ideally, several censuses utilizing both aircraft should have been conducted within a short period of time immediately after or before the ground count. Accuracy and precision could therefore be determined, and bias corrections calculated based on more than one flight for each aircaft. Unfortunately, aircraft were not available. The last two flights (Table II.2) show that repeatability is high, indicating that such error may not be great.

The efficiency of counts from aircraft appeared positively related to animal densities. The estimate of hippopotami outside the Reserve may therefore be high, as densities have increased over the two northern sectors. Bias corrections were high for these sectors, as densities of hippopotami were low during the ground count and initial flights. A bias-correction factor for a section of river

exhibiting low hippopotamus densities will have a high value (Table II.3). It follows, that if the animal density changes between counts, the bias-correction factor used to provide an estimate may not be accurate. The river north of the Reserve is markedly different from the three southern sectors, with faster currents and larger, more sweeping meanders. The influence of riparian vegetation on the correction factors may be considerable, but insufficient data are available, as only one heavily forested section was walked (sector E) during the ground counts. Observer familiarity with group locations and numbers should not have greatly affected counting bias, considering the length of river censused (124 km). An effort was made to count only those hippopotami visible from the aircraft, and not to include known group sizes for the few groups familiar to the observer.

Small single-engined aircraft were best suited for the speed and maneouverability required in order to follow the river closely and provide time for accurate counts of groups. Dividing the length of river to be counted into short sectors, with bias-corrections for each, lowers the error arising from density-dependent counting accuracy, as well as any error due to different river morphology or terrain. Frequent landings for recuperation from airsickness also helps maintain consistent count accuracy. Time of day should remain constant between flights.

Table II.3. Comparative results of 1980 ground count and corrected 1982 aerial counts (averaged) of hippopotami within the Mara River.

Sector	Year	Corrected Number of hippopotami	Observed mean group size	Sector length (km)	Corrected Density (hippopotami/km)
A. Tanzanian border to south of Governor's Camp	1980	808	10.0	38.6	20.9
	1982	969	7.8		25.1
B. Governor's Camp forested area	1980	888 *	-- *	31.4	28.3
	1982	797	10.4		25.4
C. Wooded section to north border	1980	94	13.4	4.2	22.4
	1982	57	17.0		13.6
Sub-total for Reserve	1980	1790	12.5	74.2	24.1
	1982	1822	8.8		24.8
D. North Reserve border to Buffalo Camp	1980	189	6.5	20.9	9.0
	1982	424	9.6		20.2
E. Buffalo Camp to Emarti Bridge	1980	153	12.8	29.3	5.2
	1982	573	9.4		19.2
Sub-total outside Mara Reserve	1980	342	8.6	50.2	6.8
	1982	997	9.5		19.8
Grand total	1980	2132	9.9	124.2	17.2
	1982	2819	8.9		22.7

* 1980 - Data from ground count. Section B not ground counted. Estimate derived from aerial count from Cessna times overall correction factor for other sectors.

1982 - Averaged results from two aerial counts (corrected).

Populations and Distributions

The annual rate of increase of hippopotami within the Masai Mara National Reserve was 16.5% from 1959 to 1971 (Darling 1961, Olivier and Laurie 1974), 10.3% from 1971 to 1980 (Karstad *et al.*, 1980), and 0.9% from 1980 to 1982 (Fig. II.5). Darling's (1961) estimate of hippopotamus numbers within the Mara River is evidently based on a short section of the Mara River, though it agrees with information supplied by Dawson (pers. comm.), a professional hunter familiar with the area during the 50's and 60's. Historical data for the upper reaches of the Mara River are not available.

Hippopotamus densities within the Serengeti National Park were 5.5 animals/km of river higher than within the Mara Reserve in 1971 (Olivier and Laurie 1974). The population status to the south, within the Serengeti National Park, could not be determined as access to Tanzania was denied. As there is no evidence to indicate a differential rate of increase between the Serengeti and Mara populations, it is assumed that the densities within the Serengeti do not allow for a substantial overflow to the south for the expanding Masai Mara population. The opposite has occurred, with redistribution in a northerly (upstream) direction. The present distribution appears to define an upper limit for densities of around 25 animals/km of river, resulting in a large movement of animals upstream over the two years.

Although the overall increase for the 124 km census stretch equals 12% per year, only a 0.9% annual increase is evident within the Reserve for the 1980-82 period (Fig. II.5). North of the Reserve, an annual increase of 70.5% was observed. The redistribution of densities over the period from 1980 to 1982 indicated that the river north of the Reserve has received an amount close to the increase for within the Mara Reserve, assuming a 12% annual intrinsic increase for the Reserve stretch of river.

The movement of animals from areas of high to low density may be behaviourally-directed. High densities of hippopotami result in correspondingly high levels of aggression (Attwell 1963). This is primarily determined through group size, with the territorial behaviour of the dominant males within groups resulting in fixed spatial requirements for both the group and the displaced subdominant males.

The altered rainfall patterns experienced in the Mara and Serengeti area during the past decade have apparently removed the forage-related constraints that would normally be imposed during the dry season. This probably explains the recent rates of increase, but the initial rates may have been the result of decreased inter-specific competition for forage. From the late 1800's through to 1960, rinderpest epizootics, often on an annual basis, reduced the area's ungulate populations (Sinclair and Norton-Griffiths 1979). As clinical symptoms of this disease have not been reported

Figure II.5 Recorded increase of hippopotami within the Mara River inside the Masai Mara National Reserve (Fig. II.1; sectors A, B and C).

in hippopotami (Plowright *et. al.* 1964), the impact of rinderpest could have opened a greater proportion of food resources to the population followed by a further expansion in the present post-rinderpest period, through the altered rainfall regime.

Though the time-frame was short, the section of the population residing within the Masai Mara National Reserve appears to be stabilizing in size. This trend is not apparent over the entire census population, as expansion to the north compensated for decreased growth within the Reserve. This suggests a density-dependent mechanism determining distribution, but provides little insight to ultimate population regulation.

HABITAT ASSOCIATIONS

Introduction

The habitat requirements of river-dwelling hippopotami can be considered in relation to two major environmental components; those potentially fulfilled by either the aquatic or the terrestrial habitat. Density distributions along the river evolve from a combination of these two factors, though it can be expected that the more complex habitat, as perceived by the hippopotamus, will command a greater role in the distribution of the population.

Foraging habitat is provided by grasslands proximal to the river, as the hippopotamus forages extensively on land, and primarily on grasses (Ansell 1965A, Young 1966). Though feeding almost exclusively upon grasses, the hippopotamus is considered a non-selective grazer (Field 1970). Habitat requirements on land can be considered broad, and easily satisfied within the Mara-Serengeti ecosystem. Selection for specific foraging habitat cannot be expected to greatly influence the riparian distribution of the Mara River hippopotamus population. Within the river, the day-living focus of hippopotami, the habitat is more complex. The dynamic nature of the river, with fluctuations in depth and current, and the physical and social requirements of hippopotami result in a high degree of spatial selectivity.

This chapter presents an analysis of habitats available along and within the Mara River, southwestern Kenya,

evaluated in terms of observed hippopotamus distribution and densities. A quantification of range and riparian habitats in terms of hippopotamus occupancy, should indicate the limitations of the riparian environment along and within the Mara River.

Methods

Analysis of Terrestrial Habitat

KREMU's "Habitat Types of the Mara-Narok Area" (Epp and Agatsiva 1980) maps the locations and extents of 50 habitat types. Classification was based primarily on morphologic vegetation structure delineated from aerial photos and satellite imagery. Eleven habitats are identified within three km of the Mara river for the 124 km study stretch. The foraging radius of hippopotami from water is considered to be roughly 3 km (Laws 1963, Pienaar *et al.* 1966, Lock 1972, and Olivier and Laurie 1974). Thus, a 6 km wide strip of land bisected by the river was divided into 24 subsections containing 5 linear km of river each. The areas of each habitat type within these sections were quantified using an electronic planimeter. The number of hippopotami per subsection of river was determined from aerial counts made in August and September 1982 (Chap. 2).

A step-wise multiple regression analysis of habitat type and area, with the number of hippopotami per subsection as the dependent variable was applied in order to

investigate the relationship between density and habitat types. Strong associations may suggest the foraging opportunities are important to hippopotami.

Analysis of Aquatic Habitat

River width and current measurements were taken over a 10 km stretch of river north of the Reserve. Four sessions (on different days) involving 20 measurements spaced 500 m apart provided 80 measurement points at 125 m intervals. An optical rangefinder was used to measure a 50 m stretch of riverbank, with river widths recorded at both ends. Flow was determined by timing the progress of a stick thrown into mid-stream over the 50 m stretch. Data on river depth were not obtained. Presence of hippopotamus groups were recorded if they occurred within the 50 m section.

The effect of river width and current on the location of hippopotamus groups was investigated through a series of *t*-tests, the presence or absence of groups in measurement sections was compared with river width and current.

The relative meander of the river was recorded from a 1:50000 map by measuring the straightline distance between the boundaries for the 5 km of river within each subsection. The 5 km of river divided by the straight-line distance between subsector boundaries. Regression analysis was applied to investigate the relationship between meander and hippopotamus densities.

Pool occupancy was recorded on a monthy basis for a 10 km stretch of the Mara River. Numbers within pools were also recorded during each behavioural observation period, providing supplementary data. River level was recorded at the field camp daily. Regression analysis was applied to observed number of hippopotami at "Main Pool" (the largest pool in size and hippopotamus occupancy within the 10 km study section), and water levels for each observation day.

Results

Diurnal habitat, the river, appeared the dominant determinant of hippopotamus distributions. Stepwise multiple regression analysis of adjacent vegetative habitats within 3 km of the river revealed low correlation with observed distributions of hippopotami. Though analysis was based on diurnal distributions recorded from aerial counts, the spatial limitations imposed upon hippopotami, in terms of grazing radius, limit foraging habitats to areas proximal to distributions along the river. Thus, the effects of selection for foraging habitats could directly influence the distributions of hippopotami within the river. However, such a relationship was not observed.

Land

Table III.1 presents areas and descriptions of the 11 habitat types found adjacent to the river. Fig. III.1 illustrates the percent distribution of major physiognomic

habitat types.

Correlations of hippopotamus densities per 5 km of river with adjacent habitats were generally nonsignificant. Of 11 habitats delineated by Epp and Agatsiva (1980) occurring within 3 km of the Mara River, a combination of three provide the highest stepwise multiple regression correlation:

$Y = 93.59 + WG \times 22.16 - 71.32 \times ESC - 126.22 \times WL$ ($r^2 = .486$ $p = 0.009$).

These are wooded grassland (WG), escarpment (ESC), and woodland (WL), comprising 18.9% of the total area representing hippopotamus grazing range. The equation indicates a positive association with wooded grassland, and negative associations with escarpment and woodland.

Simple correlations were significant ($P < .05$) for wooded grassland ($r = .619$), shrubby grassland ($r = -.492$), and woodland ($r = -.481$).

River

An analysis of variance between measurement sessions for width and current along the 10 km of river examined indicated that the four sessions differed significantly ($P < .05$) as a result of unequal water levels (river stage). Session data could therefore not be pooled. Table III.2 presents river width, current measurement and water levels for each of the four measurement sessions. Data are detailed in Appendix 1.

Table III.1. Areal extents of vegetative associations from habitat classes identified by Epp and Agatsiva (1980), found within 3 km of the Mara River along the 124 km study section.

Habitat	Characteristics	Area km² ...	Percent
WOODLAND-FOREST	Canopy > 20%	(8.8)	(2.2)
woodland	homog., trees > 10 m tall	8.8	2.2
SHRUBLAND	Canopy > 20% 6-10 m tall	(47.8)	(12.2)
shrubland	homog., shrubs and trees	47.2	12.0
thicket	canopy > 80%	0.6	0.1
GRASSLAND	Woody < 20%, Herbs > 20%	(275.4)	(70.1)
grassland	homog., primarily herbs	57.2	14.6
wooded	scattered trees, > 20%	48.4	12.3
shrub	shrubs/trees 1-10 m, > 20%	145.3	37.0
dwarf-shrub	semi-desert areas	24.5	6.2
RIVERINE*	Within 50 m of watercourse	(44.0)	(11.2)
wooded	trees > 10 m tall	41.5	10.6
shrub	mainly woody veg. 1-6 m tall	2.6	0.7
ESCARPMENT	Rocky, incl. some plateau	(17.0)	(4.3)
escarpment		17.0	4.3
	TOTAL:	393.0 km²	

* Riverine vegetation is dense, defined by species affiliation and intitial establishment within 50 m of watercourse (see Epp and Agatsiva 1980).

A significant ($P<.05$) relationship between river width and the presence of hippopotamus groups only at moderate water levels were indicated by *t*-tests. The two measurement sessions taken during extremely high and extremely low river stages exhibited no relationship between current speeds, width, and the presence of hippopotamus groups.

The effect of depth on pool selection by hippopotami was examined primarily by relating pool occupancy to daily water levels. Fig. III.2 is a schematic of Main Pool. Main Pool was occupied during all seasons, and had the highest number of animals for one pool recorded within the 124 km study section. The relationship between river water levels and Main Pool occupancy is illustrated in Fig. III.3. Regression analysis on occupancy of Main Pool with water level indicated a strong correlation ($R^2=.602$, $P<.05$).

Relative meander was correlated with habitat type. A stepwise regression analysis of habitat on a 5 km subsection basis, with relative meander as the dependent variable, produced a high correlation with shrubby grassland and shrubland ($r=.928$). These two habitat types were associated with low meander. Meander was also correlated to hippopotamus densities within subsections ($r=-.387$, $P<.05$). This indicated that areas adjacent to straight river channels were not heavily used by hippopotami. The straightest section of river was along the base of the Siria escarpment and contains rapids for the most part. The lack of pools and the strong current provided poor hippopotamus

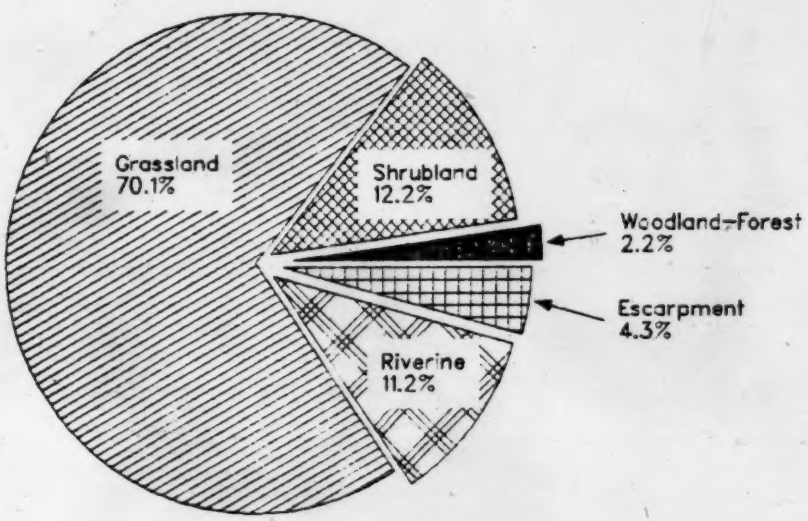

Figure III.1 Major habitat types within a 6 km swath along 124 km of the Mara River (based on Epp and Agatsiva 1980).

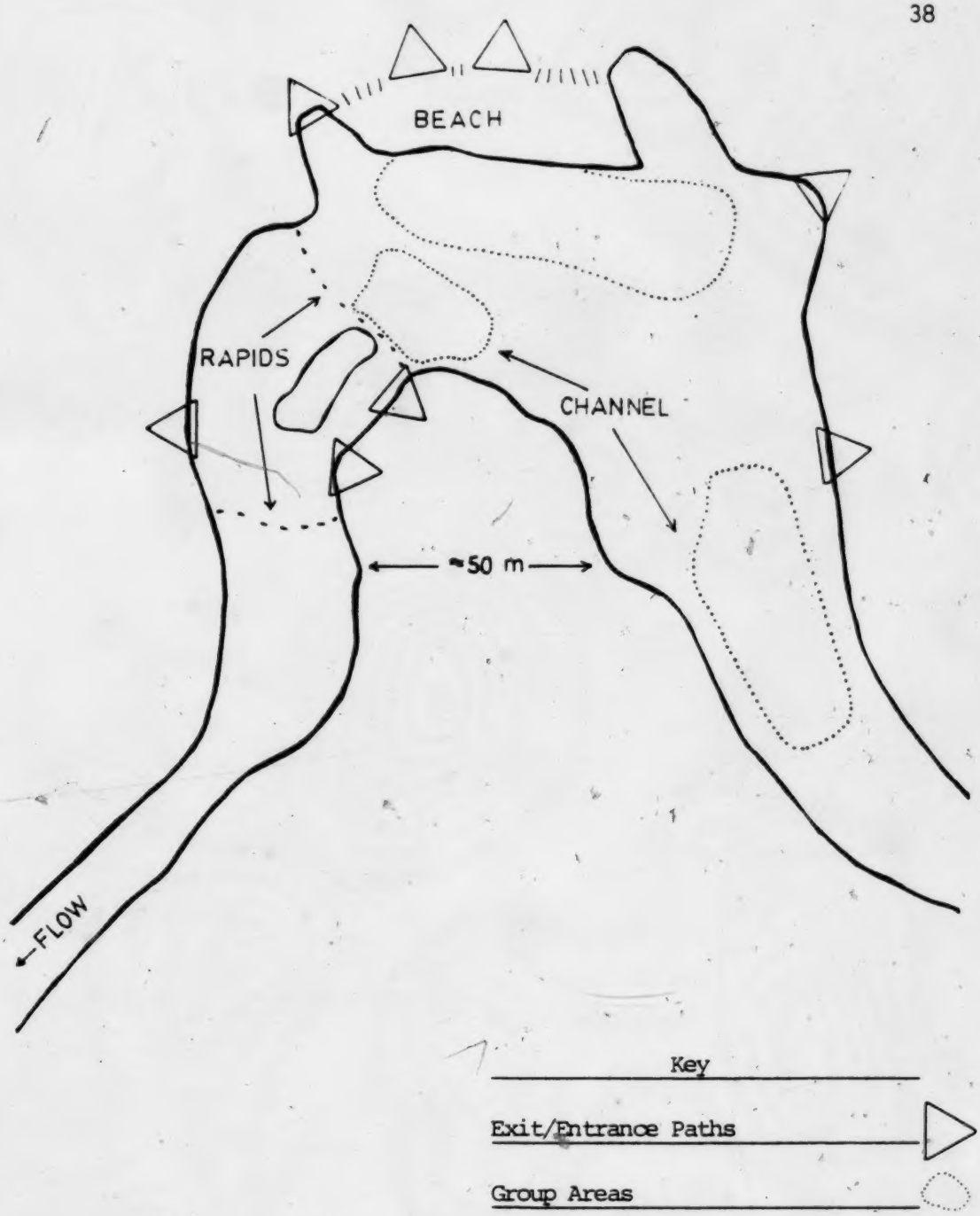

Figure III.2 'Main Pool' schematic, illustrating exit/entrance paths and group areas. Numbers of hippopotami ranged from 23 to 171 during 1982.

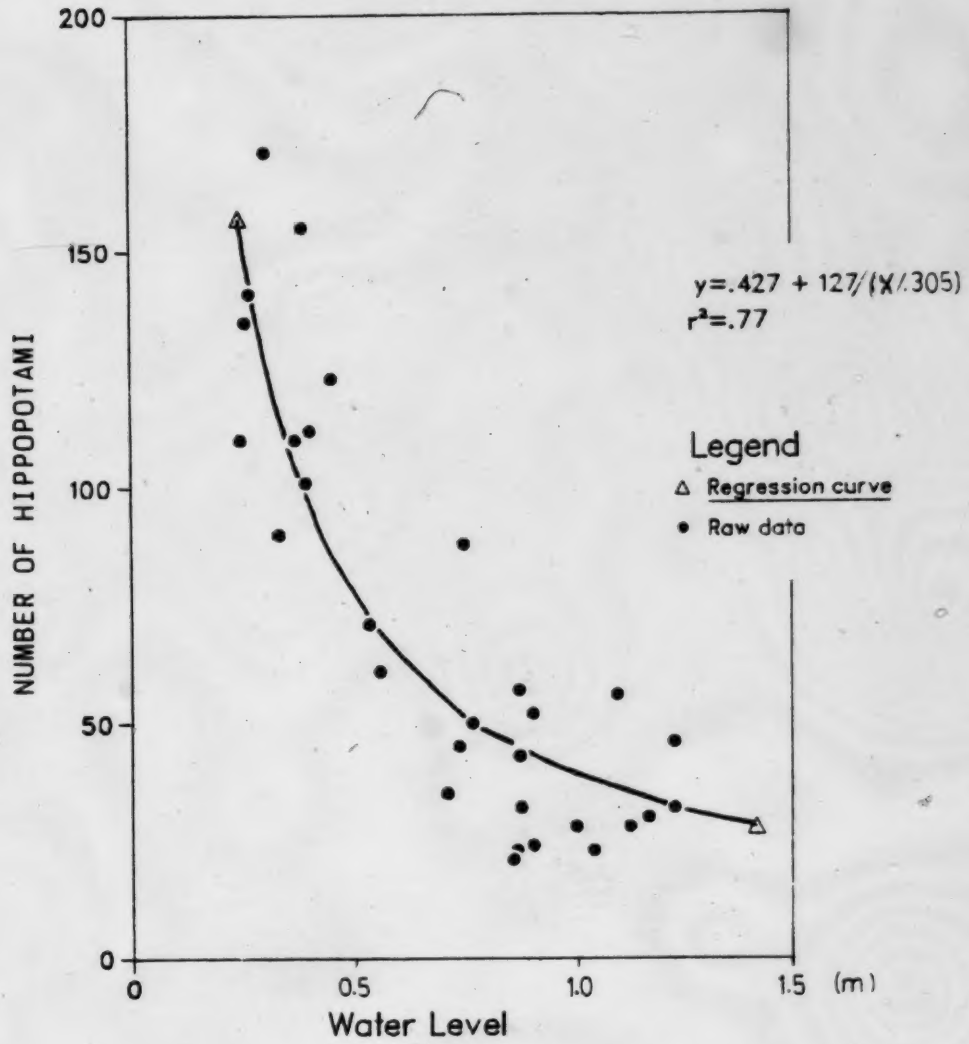

Figure III.3 Occupancy of 'Main Pool' by hippopotami as influenced by water level in the Mara River.

Table III.2. Morphometrics for 10 km of the Mara River, measured (speed and widths) over 80 50 m sections. Water levels were recorded, and 20 measurements taken per sample session.

Date (Mo/Yr)	Water Level (m)	Ave.Current (m/sec.)	S.Dev.	Ave.Width (m)	S.Dev.	N
11/81	0.70	1.07	0.48	30.72	5.74	20
01/82	0.48	0.39	0.21	26.90	4.76	20
05/82	0.88	0.71	0.25	29.13	4.39	20
06/82	1.31	1.45	0.45	32.53	4.46	20
Ave.Tots.	2.78	0.28	0.37	29.82	5.21	80

habitat. Adjacent range was sloped, providing poor water retention, and primarily composed of thicket. This area was also poor foraging habitat for hippopotami, as grass productivity appeared very low.

Discussion

The strongest environmental selection influencing the distribution of the Mara River hippopotamus population, was for the diel habitat, the pool. Locally, the suitability of specific pools was primarily determined by river depth. Observations indicated that a gently sloping beach area with available exits from the river channel, as well as a deep (>1.5 m) channel were necessary components of the optimum pool. The optimum pool allows the hippopotamus to bask in

the sun, wallow partially submerged, or completely immerse itself. Such activities evidently facilitate body temperature regulation. Flight response involved rushing into deep water in order to totally submerge.

Particularly deep river channels were avoided, as hippopotami are poor swimmers in fresh water and must walk along the bottom, surfacing for air. Some selection for pool bottom composition is suspected, as investigations of unnoccupied pools invariably revealed gravel bottoms. A moderate current would be necessary for the maintenance of a firm riverbed, particularly if the spot is occupied by hippopotami, as feces would build up if currents were slow.

During the day, hippopotami spent much of the time sleeping, usually completely submerged. Animals lay in a prone position with legs tucked under the body. A comfortable sleeping position must allow the individual to breath by simply raising it's head. Calves were found sleeping either in shallower water than adults, or supported on a larger hippo's back. Groups basked in unison, and when in shallow water all group members appeared to select for the same depth. The proportion of uniform-depth shallows within pools appeared to have an influence on the number of animals within a pool location.

Exits from the river, commonly a V-shaped path cutting into the riverbank, were most numerous in the immediate vicinity of the pool, though hippopotami may travel several hundred meters up or downstream before exiting the river at

dusk. Bank height seemed not to be a deterrent to path establishment. Hippopotami were not adverse to plunging over banks up to 4 m in height when in flight.

River width and current speed, as recorded, were not accurate descriptors of pool sites. Methods used to assess current speed were not accurate on river bends where the maximum current occurred to the inside of center, or for broken channels with backwaters behind obstacles. Width by itself did not predict depth or current, though suitable pools were generally found on wider than average sections of river, particularly on river bends. A hippopotamus group would create it's own backwater when in a current, and when lying down appeared indifferent to water velocity. Backwaters occurring behind obstructions in the river were favoured by animals separate from groups; batchelor males or females with neonates.

Analysis of densities for the 124 km study section revealed higher densities of hippopotami within subsections with repeated meanders. Overall, the river was significantly more convoluted within the Masai Mara National Reserve than to the north.

The selectivity exhibited by hippopotami for river habitat may be fortuitous in terms of forage availability. Shrubland and shrubby grassland were semi-arid habitats strongly correlated to sections of river with little meander. Along stretches of river with a high degree of meander, primarily within the reserve, were found ox-bow

lakes, marshes and lush grass growth associated with water tables close to the ground surface. Dry season forage availability was considered the greatest forage-related limitation for the hippopotamus (Bere 1959, Lock 1972, Eltringham 1974, Olivier and Laurie 1974 and Vilijoen 1980). Along the Mara River the greatest hippopotamus densities occurred in areas supporting the highest quality and quantity of vegetative biomass.

The hippopotamus is a non-selective grazer (Field 1970). A strong selectivity for vegetative habitat would therefore not be expected. What is expected, and has been demonstrated, was a selective response to diurnal habitat, primarily due to the dynamic nature of the Mara River.

Selection for sites within the river may have been based initially upon specific channel morphology, beyond that a series of social constraints regulated occupancy. As selection was strongest for day-habitat, there may not have been forage-related constraints imposed upon the population. This presents the possibility that social constraints evolving around the most important feature of the hippopotamus' ecology, the pool, may act to limit further population growth. Such regulation may act in the absence of an adequate supply of pools, and result in a large amount of aggression-related mortalities.

SOCIAL ORGANISATION AND COMMUNICATION

Introduction

The role of aggression in population regulation was first proposed by Verheyen (1954), who considers adult males to be the primary enemy of young. Attwell (1963) and Olivier and Laurie (1974) correlate increased aggression with higher mortality rates in all age classes during environmental stress, such as severe crowding within pools and/or poor nutritional regimes. In the absence of forage-related stresses upon the Mara River hippopotami during this study, there was little or no correlation between group size (day-living-space) and aggression. The question remains, that should the population continue to increase in size, will social constraints act to limit population growth? Knowledge of the social structure and dynamics of the population is essential.

The basic social unit within hippopotamus populations is the mother-young unit. Groups are composed predominantly of adult females, their calves and subadults. Several adult males may be included in the group, although there is usually a single dominant male (Verheyen 1954, Olivier and Laurie 1974, Klingel 1979).

Batchelor males, generally evicted from parental groups at puberty, 7-8 yrs of age (Dittrich 1976, Skinner *et al.* 1975), may remain solitary or join groups predominated by males (Klingel 1979, Attwell 1963). Batchelor groups are

also contained within a single dominant male's territory (Klingel 1979). Klingel (*op. cit.*) notes that solitary males inhabiting and defending stretches of river may not be as unsuccessful in attracting females as the casual observer would infer. Changes in water levels result in group movements, particularly on a seasonal basis. Hence, territories occupied by solitary males during, for example, low water levels, may contain a group of females and their offspring during high water levels.

Apart from direct aggression, communication involves sight (postural signals), olfaction (primarily dunging behaviour), and vocalization. The behaviour of dominant adult males is described in detail by Hediger (1951), Verheyen (1954), Olivier and Laurie (1974) and Klingel (1979). All authors identified two major ritualized social signals; gaping (or yawning) and dung spraying as signals in advertising and reinforcing dominance. The function of inland dung heaps is not known, though it is thought that they are maintained exclusively by adult males (Grzimek 1972) and may aid in navigation at night (Olivier and Laurie 1974).

The behavioural observations made in this study, were conducted in order to 1) describe social organisation and communication, and 2) determine if density-dependent agonistic interactions were implicated with intrinsic population control.

Methods

Group Composition

Behavioural data were collected during 196 hours of direct observation. Only toward the latter part of the field program was I able to accurately identify the sexes of adults, enabling sex and age class composition of a group to be recorded. Subadults and young were impossible to sex when in the water and were rarely seen on land.

Sexual dimorphism in adults is apparent to an experienced observer, even when only the head of an animal is above the water (Fig. IV.1). Dimorphism was manifested in the large, more heavily muscled head of the male, particularly between the eye and the ear at the insertion of the masseter muscle. Thus, the mature male had a less bulbous eye than the female. Males also possessed thicker and longer lower canines that visibly distended the cheek pouches in which they were contained.

Comparison of head length (snout to ear) provided criteria for age classification. "Subadult" head lengths were 1/3 to 2/3 the length of the head of the largest member of the group, "young" head lengths were less than 1/3. "Adult" included all members with head lengths greater than 2/3 the length of the largest individual's head.

A

B

Figure IV.1 Typical head morphologies for (A) adult males, and (B) adult females, illustrating dimorphic traits used in determining sex.

Individual Identification

A photographic card index was made of all individuals within three major groups during the first week in September 1981. A 35 mm camera, a 600 mm Novaflex telephoto lense, and high speed black and white film were used to record an image of the right side head profile (Fig. IV.2). From the photographs, an individual identification key was developed based primarily on eye-wrinkle patterns. Distinct markings such as scars and notched ears were noted. This system, though capable of identifying any individual included in the key, was used mainly to verify the identification of dominant males within groups.

Behavioural Observations

Two-hour behavioural observation periods, 112 of the 196 of which were from 1630 hrs to 1830 hrs, were conducted from September 1981 to September 1982. Though not strictly scheduled, an effort was made to concentrate observations during times of extreme river levels. This was done to compare behaviour between different levels of pool occupancy. The seasonal effects of river level on day-living-space was investigated in this manner.

Each two-hour observation period was divided into ten minute intervals. The following behaviour patterns were recorded:

1) Fights: Aggressive interactions classified to three levels of severity;

Figure IV.2 Example of an individual identification photograph illustrating the eye wrinkles (A, B, and C), and a triangular area (D), used in the identification key.

Class 1: Rush or jump, short, may be a slash from behind. Not always involving physical contact.

Class 2: Frontal slashing with contact, or a persistent (> 3 second) chase with or without contact.

Class 3: A protracted fight, physical contact with visible wounds and bleeding.

2) Gapes: All group members included.

3) Vocalizations: Recorded for both the number of sessions and the number of animals participating in each.

4) Submissive defecations: Cumulative for 2 hr observation period, recorded regardless of age class involved.

5) Mark defecations: Cumulative for 2 hr observation period, with special note made if involving an animal other than the dominant male of the group.

Water Levels

Water levels in the river were recorded at 0900 hrs daily. A staff gauge was firmly sunk in hard clay and attached at the top to the base of a large tree. The data obtained are relative only, the gauge was not tied to a known elevation through survey methods, nor were the morphometrics of the adjacent river channel determined. The volume of water flow at the gauge site could therefore could not be calculated.

River dynamics were determined from daily water level records and divided into increasing, decreasing, static high

and static low conditions. 'Increasing' and 'decreasing' involved a constant change in river level of greater than five days duration, resulting in an overall change equal to or greater than 0.33 m. Low and high 'static' conditions do not meet the above conditons and were for low, less than 0.6 m in height, and greater than 0.6 m in height for high, as measured on the staff gauge.

Statistical Analysis

Statistical analyses were applied to behavioural data collected between the hours of 1630 and 1830. With the exception of matings, all forms of 'riverbound' activity were at their highest during this time.

A Pearson correlation matrix was produced from pooled session data. Observation sessions were also distributed within the four categories based on river dynamics for the day each session was conducted. As sample sizes were reduced in this manner, non-parametric analysis was adopted using Spearman's rank order correlations.

Sex and age-class-specific agonistic encounters were analysed on an expected vs. observed basis using chi-square tests. category-specific confidence intervals were calculated according to Neu *et al.* (1974). Class 3 aggression occurred very infrequently and was excluded. The hypothesis tested was that aggression initiated by each class was proportional to their numerical representation.

Results and Discussion

Group Stability and Movement

The average group size was 13.3 individuals. Adult males comprised 8.0 percent, adult females 36.2 percent, subadults (not sexed) 27.0 percent and young 28.8 percent. These data reveal a low proportion of adult males, reflecting the exclusion of rivals from groups by the dominant male. Data collected were from female-offspring groups only. Very few 'batchelor groups' (Klingel 1979) were noted within the Mara River non-dominant adult males appeared to prefer a solitary existence. Individuals not associated with groups were noticeably less attached to specific sites. Klingel's (*op. cit.*) observation that both batchelor and female groups were rarely of a homogenous composition, held true for the Mara River population.

Territories of dominant males were first thought to include not only stretches of river or lake shore, but pear-shaped inland grazing areas delineated by dung heaps (Hediger 1951). This observation has since been discounted by Verheyen (1954), Olivier and Laurie (1974) and Klingel (1979). Territories in pools have been noted and described by Klingel (1979) in Uganda. However, Olivier and Laurie (1974) noted that recognizable individuals were seen at widely different places in the river during their three month study of the Mara River system and concluded that spatial affiliations between males and stretches of river

did not exist, hence, territoriality did not occur.

Strong site attachment by dominant males existed, though river dynamics dictated the placement of female and their offspring, with invariably a specific dominant male for each pool site. The unsuitability of pools at particular river levels commonly caused the associated dominant male to leave when the group dispersed, often joining a small group in a nearby, more comfortable pool. On three occasions a dominant male was observed to follow a group of females from "his" site to an adjacent pool and assume a subdominant position in deference to another male. Once water levels returned to acceptable depths, males would return. This flexibility does not preclude territoriality, as concluded by Olivier and Laurie (1974). Owen-Smith (1977) includes the submissive behaviour of territorial bulls outside of their territories as a typical behavioural trait common to most territorial ungulates. The 'Evolutionary Model' presented by Owen-Smith (*op. cit.*) presents population classifications that lead to the evolution of territoriality. From spatial limitations to weapons morphology, territoriality is the logical system for regulating access to breeding opportunity within hippopotamus populations.

The territorial behaviour of lacustrine hippopotami appears much more rigid than that of riparian dwelling hippopotami. Klingel (1979) records a single dominant male holding the same territory for 8 years. Tenure of territories, according to Klingel (*op. cit.*), is markedly

different for lake and river bulls. His records indicate that the average tenure for lake hippopotami is 4.5 years; for river hippopotami a few months only.

Records for the Mara River were more conservative. During 18 months of study, only one dominant male was observed to have been permanently displaced by a rival, subsequently dying from wounds inflicted in the decisive battle. One male was positively identified as having tenure at Main Pool from August 1980 to September 1982.

The confusion generated by previous authors over the territorial aspects of dominant males (Hediger 1951, Attwell 1963, Olivier and Laurie 1974, and Klingel 1979) appears to be the result of intermittent site attachment resulting from river dynamics. Fig. IV.3 illustrates the movements of one group of hippopotamus over 3 pools along 750 m of river. Each site was claimed by a different adult male when water levels were at a suitable level for occupancy.

Redistribution in response to water levels occured not only at the specific pool and group level, but over long stretches of river as well. Fig. IV.4 illustrates the number of animals within a 10 km river section as related to month and water levels. Apparently, less favourable conditions (most likely fewer suitable pools) were encountered both up and downstream of the study section during the dry months. Low water levels in the river were the most apparent cause of the influx, but the possibility of movement dictated by forage availability and/or adjacent human activity cannot be

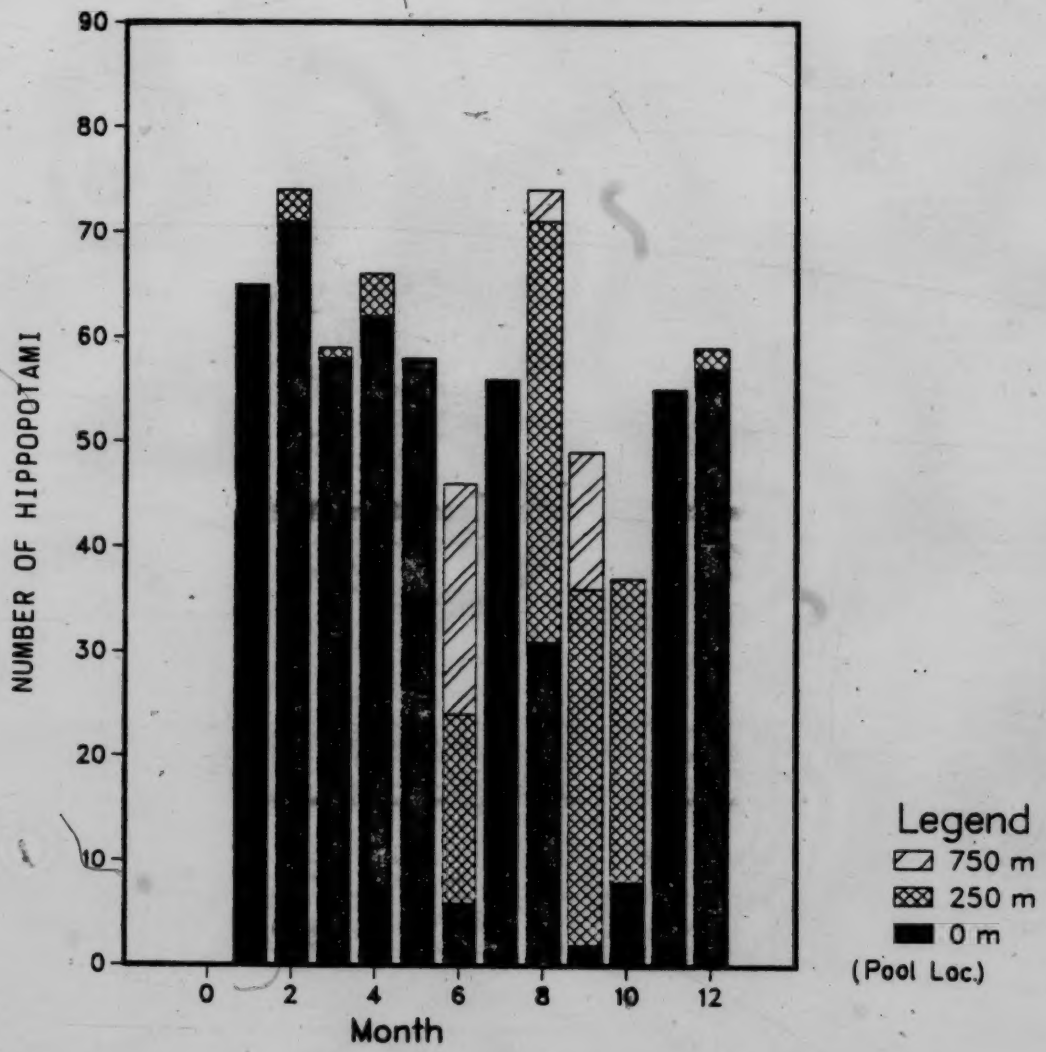

Figure IV.3 The monthly distribution of group '1' hippopotami over three locations; 0, 250, and 750 m from the most downstream pool within the Mara River study section.

excluded.

Second to the basic unit, the mother-young association, is the pool association. Based on individual identification, no temporal and spatially consistent alliances between two non-related conspecifics were observed, though each major group seemed to have a core of individuals that could always be found together when pool sites changed. The fluctuation in numbers of hippopotami at Main Pool (from 29 to 171) over the duration of the study was the result of contraction and dispersal of individuals over at least nine peripheral pools. Small groups were unstable in composition.

There was no evidence of any type of purposeful migration. The furthest point between observations of an individual animal within the river was 1.2 km. The northern thrust of density redistribution along the Mara River (Chap. 2) may very well be the result of the movement of individuals without strong site attachment. Solitary subadults, assumed to be males, were commonly seen adjacent to groups, and received the brunt of aggression from adult group members. These individuals quickly left sites when disturbed.

Agonistic Behaviour

Analysis of observed/expected aggression initiated by each age class, showed significance ($P<.05$) for adult males and calves (Table IV.1.). Adult males initiated a disproportionately high number of agonistic encounters, and

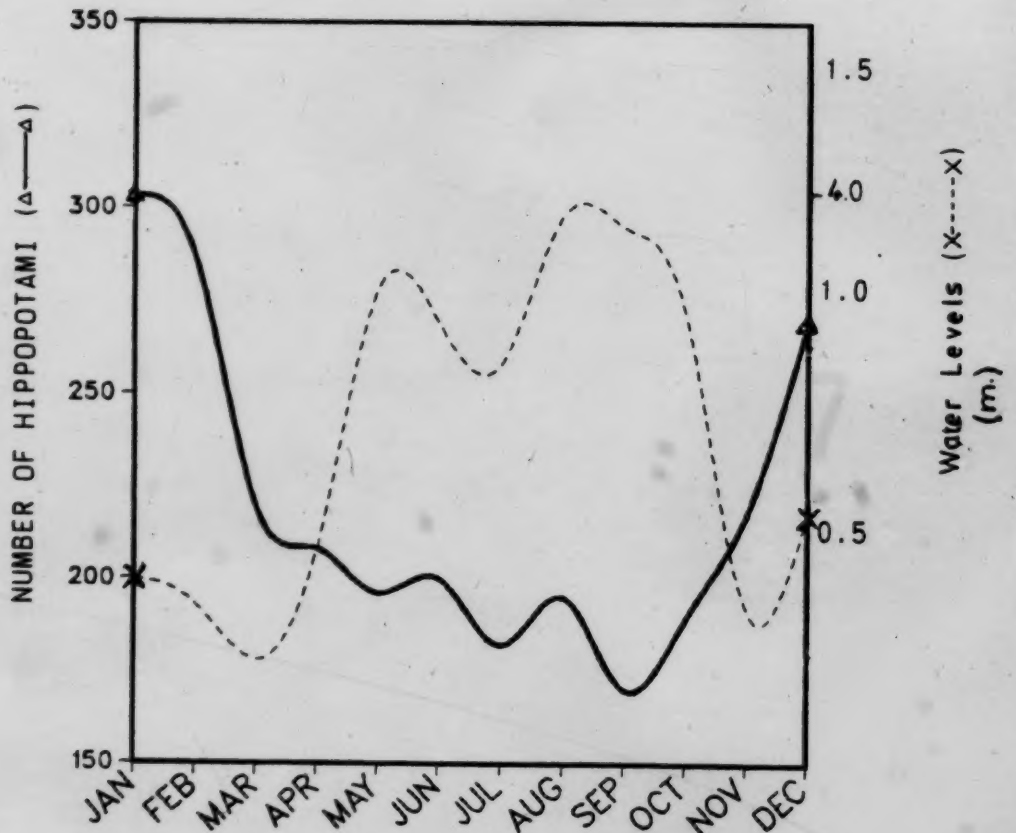

Figure IV.4 Water levels in the Mara River and the corresponding number of hippopotami within the 10 km study section. Data are from averaged monthly records from 1981 and 1982.

calves initiated a disproportionately low number(Fig. IV.5). The agonistic behaviour of adult group males and females appeared strongly implicated with the expulsion of subadult males. Combined data from Table IV.1 for the aggression of adults towards subadults amounted to 32% of all agonistic encounters. This corroborates previous analysis of age of puberty and age at expulsion from groups (Dittrich 1976 , Skinner *et al.* 1975). Lone subadults as well as a proportion of those in groups exhibited fresh scars during all seasons. The three severe (class 3) fights observed were between adult males. In all cases, the dominant group male fought and chased off an intruder. The reverse-parallel stance reported by Leuthold (1977) and Klingel (1979) assumed during serious fights between rival males was not observed, though prolonged ritualized displays involving gaping, splashing, vocalizations and marking defecations, preceded physical contact. Such conflicts were always observed to occur as a result of a foreign male's intrusion into a stretch of river containing a territorial male. Territoriality reduces conflicts between dominant males, an important consideration when potential for damage from fights using the long, sharp, canines is great. Ritualized encounters are expected between ungulates possessing potentially dangerous weapons (Giest 1966).

Correlations between aggression, water levels and the number of individuals within groups, for the four river dynamic states, were generally non-significant ($P > .05$). One

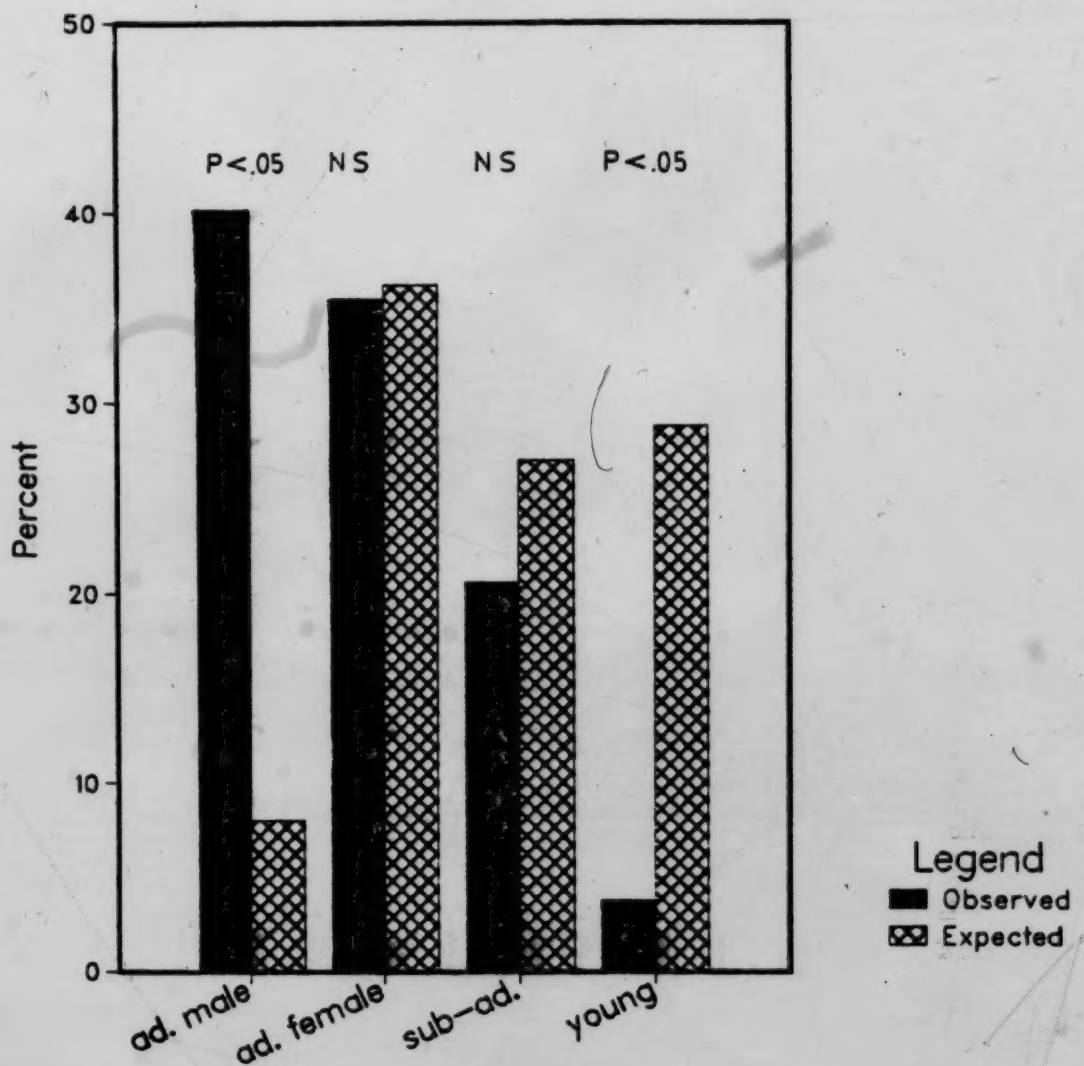

Figure IV.5 Percentage of aggressive encounters initiated by specific sex/age classes of hippopotami. Observed and expected values are shown, as well as level of significance according to Neu *et al.* (1974). All observations were made within the 10 km Mara River study section between 1630 and 1830 hours.

Table IV.1. Age and sex class-specific agonistic encounters between hippopotami classified to three levels of severity. Data were collected during 112 hours of observation, conducted between 1630 and 1830 hrs.

	AM:AM	AM:AF	AM:SA	AM:Y	AF:AF	AF:SA	AF:Y	SA:SA	SA:Y	Y:Y	TOT
F1:	10	06	17	10	14	15	09	12	10	04	107
%:	9.4	5.6	15.9	9.4	13.1	14.0	8.4	11.2	9.4	3.7	
F2:	09	00	01	00	02	04	01	02	00	00	19
%:	47.4	00	5.3	00	10.5	21.1	5.3	10.5	00	00	
F3:	03	00	00	00	00	00	00	00	00	00	3
%:	100	00	00	00	00	00	00	00	00	00	

AM= adult male AF= adult female
SA= subadult Y= young
F1= low severity F2= med. severity F3= high severity

trend is apparent; the decreasing river state resulted in the highest non-parametric correlations between both fight 1 and water level (P=.073, r=.39), and fight 1 and the number of animals within a pool (P=.023, r=.52). This indicated that the highest level of aggression occurred as groups coalesced while water levels were dropping. Lack of significant correlation during static low levels indicated that once a social equilibrium is attained aggression decreases, even during periods of high occupancy.

Correlations between aggression classes 1 and 2 were non-significant for all conditions except static low. This was also the condition in which the correlation between group size and fight class 2 attained the highest significance (P=.078, r=.39). This may mean that there was

little in common in the causes behind the two levels of aggression except at high group density.

The role of aggression in population control has not manifested itself within the Mara River hippopotamus population. Correlations with group size (day-living-space) were weak. Fights resulting in serious injury were uncommon and restricted to adults. Very few hippopotami were not extensively covered with scars, though subadults generally exhibited a greater proportion of fresh shallow cuts. Severe wounds were noted on many adult animals but comparably few subadult and young.

The apparent lack of environmental stress (e.g. drought) may have accounted for the relatively harmonious existence observed within even the largest pools. Attwell's (1963) correlation between density and high levels of aggression-related mortality is based on observations made during an extended dry season. Appendix 2 presents recorded data on mortalities observed and reported during this study.

Communication

Communication between individuals was important in maintaining low levels of overt aggression. Rarely was aggressive physical contact not preceded by a clear exchange of signals. The most obvious forms of communication between individuals involved threats, both postural and vocal, and appeared effective in maintaining a *status quo* within hippopotamus groups. The maintenance and enforcement of

dominance by a single mature male within most groups has resulted in specialized signals.

Visual Signals

Postural Communication

Posturing is an important form of communication in the hippopotamus. Several specific postures, in addition to gape, were associated with warning potential rivals of an intent or willingness to fight. Confrontations between adult males used most postures noted, though all other sex/age classes were occasionally observed posturing similarly.

Dominant males were the only group members consistently seen to have the ears in a 'cocked forward' position, a charactaristic first pointed out by Klingel (pers. comm.). Subdominants normally held the ears angled back along the neck.

The most commonly observed dominance posture was neck arching which exaggerates the size of the neck and shoulders, as well as lifting the eyes clear of the water. The nostrils usually remained submerged. This attitude was commonly used to elicit defecation displays from subdominants. The head was held in the same manner during most charges.

The subdominant posture was the converse of neck arching. The head, neck and back were maintained in the same plane. This allowed the ears, eyes and nostrils to clear the water. Ears were held angled back or down.

"Humped" postures often followed the dominant head tilt, the animal lowers its head and arches the back, and only the arched back is visible above the water. This posture clearly gives the impression of massiveness, and has been observed to precede submerged charges.

All group members were constantly aware of the dominant male's disposition. The simple act of turning the head to look directly at an animal could stimulate a subdominant to deliver a defecation display. Totally relaxed positions were assumed with the neck extended, and often individuals entering groups were halted by the dominant male leaving the relaxed position and turning the head to look directly at the intruder. It is not necessary, due to the eye placement, for hippopotamus to focus binocularly on objects, hence, this 'staring' behaviour appeared to be a form of intimidation.

Gape

Gaping was common to all age and sex classes. The specific social implications were not completely clear, though the action appeared an attention getting device. Of the several ritualized aggressive encounters observed between adult males, gapes were most frequent, and often lasted up to 10 seconds. Dominant males exhibited the most energetic gapes, and assumed a specific stance with the neck extended and the head thrown back, so that the top of the head (ear to snout) was almost perpendicular to the back. Young, probably emulating the dominant male, were the only

other age group to exhibit this particular posture while gaping. This position exposes the vulnerable underside of the neck, seemingly an advertisement of confidence. Leuthold (1977) interprets the raising of the head to a nearly vertical position, common in many ungulates, to be a strong intimidation display. Herring (1975) describes the morphologic adaptations common among suiforms that allow the gape display.

Non-parametric correlations between gape and all other recorded behaviour was non significant ($P>.05$) with the exception of one situation; dominant male gapes during static high water levels correlated with group size ($P=.021$, $r=.46$). This was due to groups being scattered and numerous during high water levels, with a corresponding high number of territories occupied. All social signals correlated strongly to group number at this time.

Gape frequency increased towards dusk as individuals prepared to exit the river to graze. The temporal distribution of gapes for dominant males and other age/sex classes are presented in Figs. IV.6 and IV.7, for the period of time between 1630 and 1830 hrs.

Gape breadth, the distance between upper and lower lips, was constantly measured between animals within the young and subadult age classes. The process involved carefully matching lips, then gaping and pushing, an activity that can be repeated for hours. Usually the larger participant 'wins' by pushing the opponent up and back.

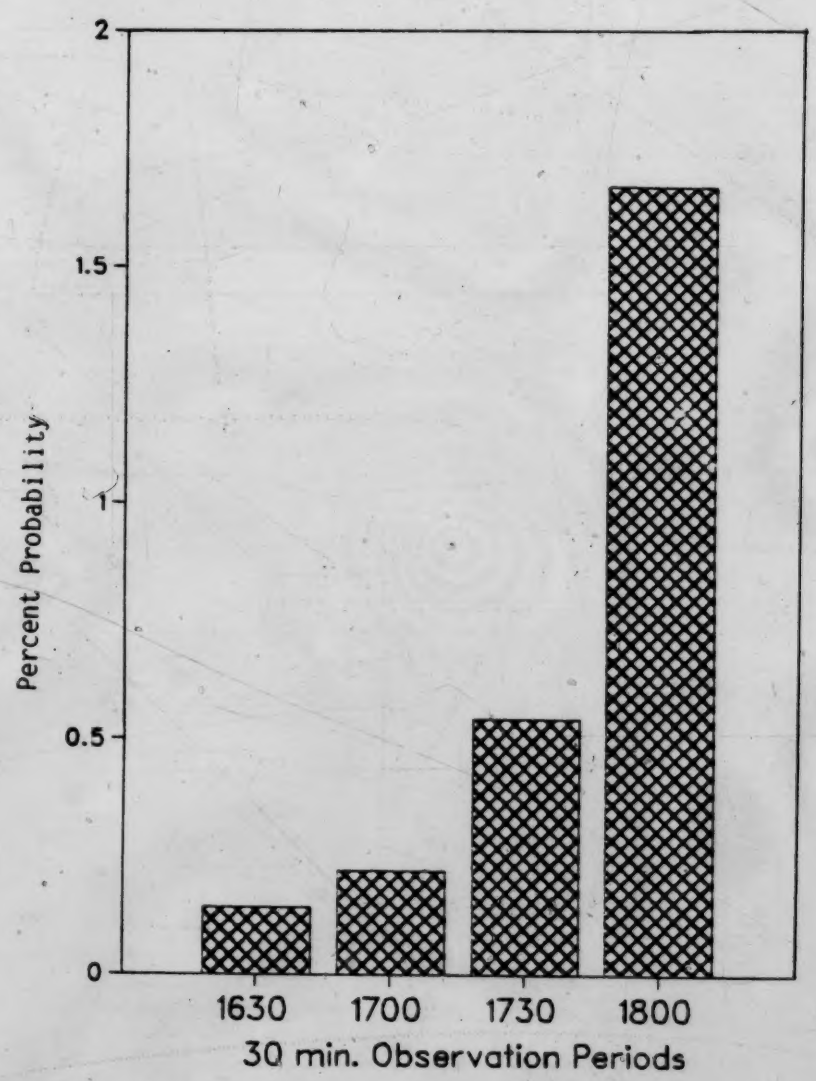

Figure IV.6 The probability of dominant male gape in the hippopotami of the Mara River, expressed as percent per 30 minute period between 1630 and 1830 hours.

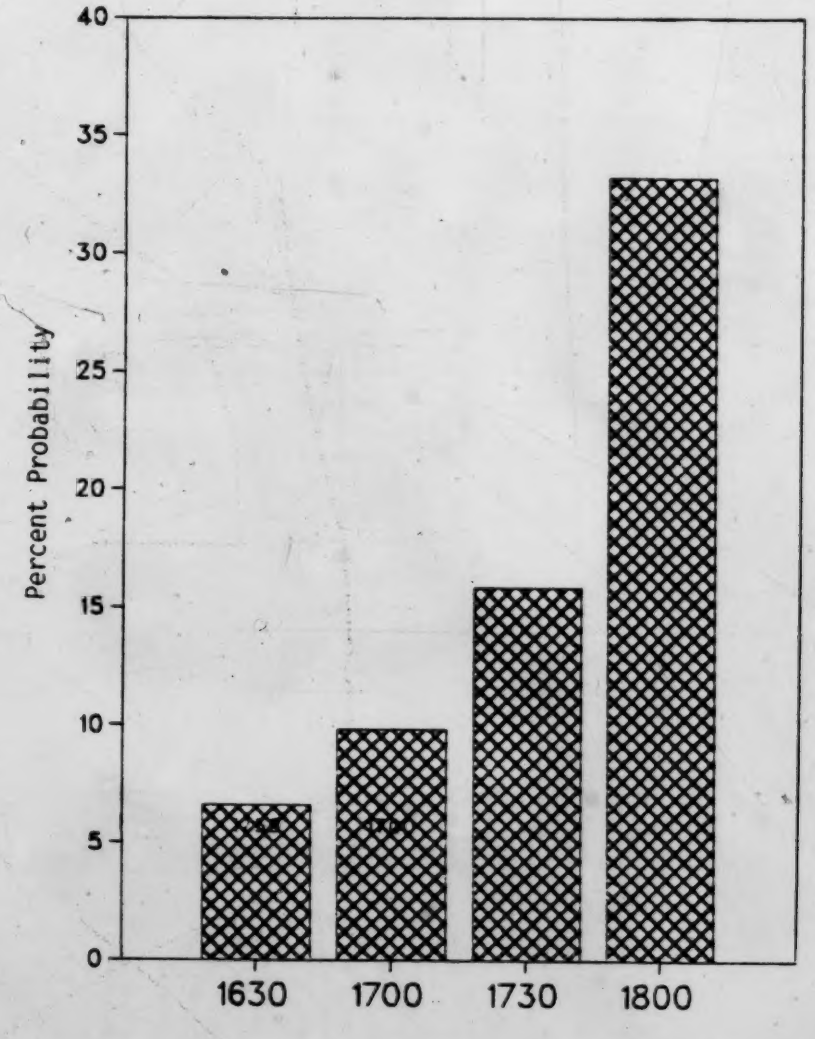

Figure IV.7 The probability of gape for all individual hippopotami of the Mara River, expressed as percent per 30 minute period between 1630 and 1830 hours.

Adult females were observed to 'lip wrestle' in this manner on three occasions, and twice the activity was observed to precede mating by the dominant group male. Whether the activity aids in establishing a group hierarchy was not determined. Weapon size, tusk size for hippopotami, is a component in establishing dominance through intimidation (Leuthold 1977). The gape display exposes tusks for evaluation. Gape breadth may be an additional rank indicator.

Vocalization

Vocalizations were common, particularly toward evening as animals prepared to exit the river to graze (Fig. IV.8). Vocalization recorded during the first time period (30 min) may be greater than the second due to the arrival of the observer. Vocalization was a standard response to any disturbance that did not force the animals to submerge.

Vocalizations were conducted in sessions, with two, to nearly the entire group participating, and consisted of a wheezing inhalation followed by several reverberating honks. This was emitted through completely dialated nostrils, not from the mouth.

Groups and individuals separated on land at night would communicate with each other by vocalization. As the sound may carry well over one kilometer on a still day (further at night), it was not uncommon to hear a chain of vocalizations from one group or individual to another along the river.

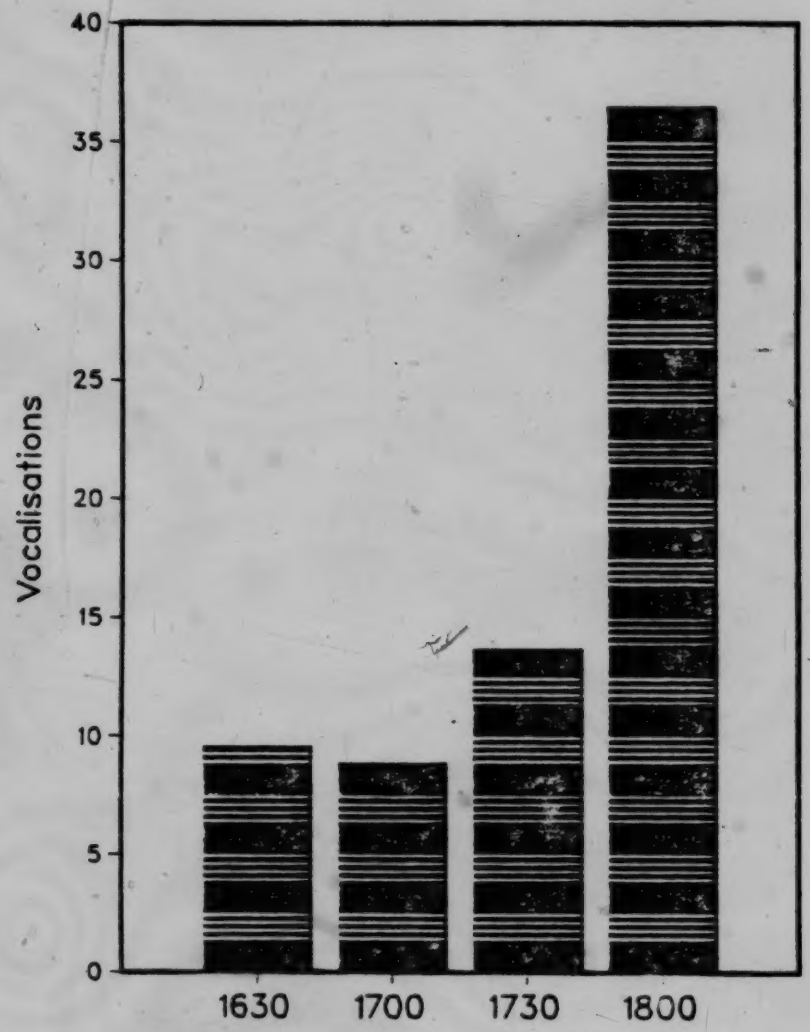

Figure IV.8 The average number of hippopotamus vocalizations within groups along the Mara River per 30 minute period between 1630 and 1830 hours.

Vocalizations during serious aggressive encounters range from sounds very similar to a lion's roar to high pitched squeals, and is usually accompanied clashing teeth. The full function of vocalizations, other than as a warning, was not determined.

Non-vocal auditory signals may be a component in the energetic splashing during most agonistic confrontations. Jaw champing conducted at these times clash teeth together, a noise that, while not loud, probably acts as an additional auditory message.

Defecation

Submissive Defecation

Submissive defecations are characterized by the subdominant animal lifting its hindquarters clear of the water and splashing water with its tail in the face of a dominant individual. The subdominant holds it's head low and extended, with ears normally laid back. Often, though not necessarily, the animal would defecate during the process. This signal is not offered exclusively to the dominant male of the group; all age classes, with the exception of very young animals exhibit this behaviour. No dominant male was observed to submissively defecate. Non-dominant adult males submit in this manner to the dominant, and it was common to observe a dominant male 'make the rounds' and elicit defecations from several animals within the group. The dominant animal would normally posture by standing with neck

and shoulders above the water and the head angled down from an arched neck. Hissing inhalations and short explosive exhalations often accompanied prodding of the subdominant animal's anal region.

Both male and female adults normally submitted in this manner to territorial males when entering a group or territory. During times of general activity amongst pool members, sub-adults would constantly defecate in the face of the dominant male without any apparent prompting.

The common denominator between receiver and submitter was size for all interactions not involving the dominant male. The proportion of submissive defecations offered to the group dominant male was recorded for 58 hours of observation (1630-1830 hrs). The average number of gestures per hour was 5.2, 33.2 percent of which were directed to the dominant male.

The result of a Pearson correlation test for all data, regardless of river dynamic state, showed that the rates of submissive defecations per individual correlated negatively with the number of animals within groups ($p=.018$, $r=.84$), and positively with the rate of "Fight1" aggression ($p=.040$, $r=.75$). The former revealed that group members were more active in social status reinforcements within small groups, the latter may indicate the function of the submissive gesture in terminating or avoiding agonistic encounters. There was no significant relationship between rates of Fight2 aggression, or river dynamic state and submissive

defecation.

Marking Defecation

Marking defecations were performed both in the water and along the bank. Only once was any animal other than a territiorial male observed to exhibit this behaviour; a lone female with a neonate expressed her agitation at being disturbed by an observer. During 112 hours of observation, 65 displays were noted (1630-1830 hrs). The action usually involved the territorial male backing up to a bank or the shore and copiously defecating, scattering dung up to 2 m in radius by flapping it's tail vigorously. Often the male is accompanied by several young and subadults showing interest, and sniffing and eating the dung. Dung scattering is also an important component in the ritualized aggression between rival males.

Non-parametric correlations were not significant between mark defecation and all other behaviour and interactions for the four river dynamic states. Pearson correlations revealed a significant correlation (for pooled data) with dominant gape, as previously mentioned.

Locations for mark defecations along the bank were visited regularly by the territorial males, and would appear to define the extent of each male's territory (Klingel 1979).

Summary and Conclusions

Statistical analysis did not indicate a strong association between aggression and crowding within pools. A seasonal trend in number and intensity of aggression (mediated through water levels) was apparent. As environmental stress, such as extremely low water levels and/or lack of forage, was not evidenced along and within the Mara River during this study, these results cannot preclude that crowding is not a component in population regulation via aggression.

Calves were commonly the victims of aggression by adults, though no mortalities were recorded. If aggression were to intensify, as would be expected during times of stress, then frequent calf mortalities could be expected. Adult mortalities were recorded, and would be expected to increase if the population were stressed, though adults through bulk alone, are much less prone to serious injury.

A true harem system does not appear to be enforced by dominant hippopotamus males. Possessive, attentive behaviour by dominant males is common toward estrous females (Verheyen 1954). Territorial animals such as the impala may possess a somewhat dynamic territory, flexibility in size and location dependent on several factors such as the number of females contained, grazing quality and requirements etc. (Sinclair and Norton-Griffiths 1979). The intermittant occupation and defense of specific sites by dominant hippopotamus males, determined primarily through river levels can be considered

to constitute a form of territorial behaviour. Klingel (1979) recorded site occupancy for dominant males in a lacustrine environment to be in the order of years. For the riverine habitat, local dominance was maintained for only months at a stretch by any single male. The major difference was the relative stability of water levels.

The role of territoriality in population growth must be left to conjecture, though territoriality becomes more pronounced in populations of high density (Leuthold 1977). In comparison with many other ungulate territorial behaviour, the behaviour of hippopotami appears both more permanent, with less frequent contests and replacements of territorial males, and less structured, for example, there was a lack of sexual homogeneity within batchelor groups. The intermittant occupation and defense of specific sites by dominant hippopotamus males, determined by river levels, can be considered to constitute territoriality. Animals such as the impala also possess dynamic territories, flexible in size and location and dependent on several factors, such as the number of females contained, grazing quality and quantity, and seasonal cycles (Sinclair and Norton-Griffiths 1979)

The Mara River supports a density of hippopotami equalling the highest densities within much larger rivers, such as the Luangwa in Zaire, yet evidences no pronounced social mechanisms that may lead to population regulation. This indicates a social flexibility, possibly regulated by

environmental conditions.

FORAGE RESOURCE LIMITATIONS

Introduction

In an ecosystem strongly dependent on resource partitioning (Vesey-Fitzgerald 1960), the feeding strategies of hippopotami are singularly generalized. Whether this non-selective grazing behaviour (Bere 1959, Marshall and Sayer 1976, Mackie 1976) has evolved in response to foraging radius restrictions or digestive characteristics has not been determined. The hippopotamus has the ability to disrupt the finely balanced interrelationships within the riparian and lacustrine environment. To what extent the ecology associated with the Mara River has been disturbed by hippopotami is the focus of this chapter, and though major detrimental impacts have not yet been exhibited, it is essential to identify density-dependent trends in anticipation of a larger population.

The most obvious consequence of the grazing behaviour of the hippopotamus is it's potential to effectively exclude large numbers of herbivores from it's grazing area during times of forage limitation (Thornton 1971). Forage limitation can be caused directly by hippopotamus offtakes, with subsequent vegetative cover loss and soil erosion.

It has long been considered that the major potential limitation on hippopotamus populations is forage availability, with intra-specific competition for the resource potentially very high (Bere 1959, Pienaar *et al.*

1966, Marshall and Sayer 1976, Olivier and Laurie 1974, Mackie 1976, Smuts and Whyte 1981). Eltringham (1974) conducted a classic removal experiment on the Mweya peninsula, Rwenzori National Park, Uganda, excluding 270 hippopotami from the 4.4 km² peninsula. His results, after 11 years of hippopotamus exclusion, were dramatic: 1) total vegetative basal cover increased from 21.7% to 57.8%, 2) litter increased from 1-2% to 42.9%, 3) total numbers of animals (5 major species) increased 54%, and 4) including the removal of hippopotami, animal biomass (5 species) increased 20%. This study demonstrated that forage resource competition can exist between hippopotami and other animal species, and that the impact of high densities of hippopotami is potentially deleterious to range ecology.

Competition for forage between cursorial ungulates and hippopotami is restricted to shared range, considered to be approximately 3 km in radius from occupied pools (Laws 1963, Olivier and Laurie 1974). The impact and extent of competition then rest on two major factors: 1) the quality of rangeland within the 3 km zone, and the dependence of ungulates upon it, and 2) the energy costs involved for ungulates to travel from areas of suitable forage availability to the river for water, particularly during the dry season (Sinclair and Norton-Griffiths 1979).

This chapter analyses the interactions between hippopotami within the Mara River and other herbivore species utilizing the rangeland adjacent to the river in

order to assess the proportional offtakes of herbaceous biomass. Distributions of both animals and vegetation in relation to season and the catena are considered. The responsiveness of forage production to precipitation and observed standing grass biomass are weighed against the requirements of herbivores within the study area. This study suggested that the hippopotami within the Mara River are dependent upon a continuation of the present precipitation patterns.

Methods

The distribution and quantity of grass available within a 3 km radius of the river, as well as the areal extent of the short-grass pastures preferred by hippopotami was measured on both a monthly and seasonal basis.

Clip plots used for calibration of a horizontal intercept technique developed for this study (Appendix 3), were collected over 14 months and were distributed evenly along 10 km of river adjacent to the field camp. Locations were systematically determined by selecting sites halfway between previously visited locations. All plots were located within 50 m of the river. The equation used to predict standing dry weight biomass was:

Biomass (dry) = -3.307 + (GND x 8.155) + (CM10 x 3.052) + (CM30 x 3.729).

Where, Gnd= the number of 'hits' made on plant basal parts (out of 50), and CM10 and CM30= the intercept levels of 10

and 30 cm respectively. The method is explained in detail in appendix 3.

Sites, once located, were subjectively assigned 1 m^2 sample plots according to grass heights. At the first 8 sites, representative long and short-grass plots were chosen, and once a third drying bag was obtained, 3 plots were clipped at all subsequent sites; high, medium and low grass heights. This was performed in an effort to reduce possible bias due to subjectivity in the selection of specific plot site once the area had been located. Allocation within height classes was dependent upon the range of grass heights within any sample site. Extremes in height were avoided, and there were no extensive homogenous grassland communities encountered.

Clip-plots provided a record of the seasonal availability of grass along the river. All samples collected were air-dried in cloth bags for a minimum of 48 hours. Weights before and after drying were recorded in grams with a spring scale.

Clip plots were not collected from a homogenous grassland community, in terms of species composition or height. Hence, determination of minimum sampling intensity was not made. The patchiness of the riverine grassland and the time-span over which samples were collected (14 months), violated homogeneity requirements necessary for the determination (DeVos and Mosby 1971).

Seasonal Biomass Measurements

Fifty locations were sampled using the horizontal intercept technique. A 60 km² area (10 x 6 km), bisected longitudinally by the Mara River, was divided into a 100 m² grid on a map and sample sites (x and y coordinates) were selected randomly with replacements.

Fifty sites on both sides of the Mara River were visited and sampled during mid short-grass season (January 14-18 1982) and mid long-grass season (June 27-30 1982). Biomass estimates were obtained by using the horizontal intercept method for each location, and the straightline distance to the river determined.

Distribution of Grazed Areas

A series of 1 km transects were established parallel with the river in order to assess the amount of preferred short-grass range available to hippopotami during the long-grass season. Following a rounded logarithmic progression, transects were established at 25 m, 75 m, 200 m, 550 m, 1500 m, and 3000 m distant from the river. During June 1981 and 1982, each transect was walked and the amounts of short (grazed) and long (ungrazed) grass were determined. Small areas of grazed grass intercepting the transect were measured using a 15 m tape measure. Larger areas were measured with an optical rangefinder, and orientation along each axis was accomplished with a compass. The number of hippopotamus trails crossing each transect were noted.

Herbivore Census

A modified strip census was conducted on a weekly basis (with some gaps) from September 1982 to October 1983. A circuit of 32.6 km was followed using existing tracks, and all animals observed within 200 m of either side of the vehicle were identified to species and counted. The circuit was established on the east side of the Mara River along the 10 km study section. Vehicular access was not possible to the west side of the river.

Censuses were conducted between of 0930 and 1200 hrs.. An optical rangefinder was used to determine distance when necessary. All data were recorded on tape and transcribed the same day. Table V.1 presents the animal species recorded and the average body weights as presented by Stelfox *et al.* (1979).

A catena, divided into three levels, was identified based on both distance from the river and subjective assessment of vegetation type. Each encompassed roughly a 1 km swath along the river, with the furthest being the 'high' catena, starting at the 2 km (from river) distance, to 3 km.

The 'low' catena, proximal to the river, contained 8.7 km of the circuit, 'medium', 17.7 km, and 'high', 6.2 km. The availability and location of tracks was the primary determinant in the proportion of the census circuit within each catena.

Table V.1 Average individual body weights (by species) used to calculate animal biomass from data collected in weekly censuses (Stelfox *et al.* 1979).

Wildebeest	123 kg	Impala	40 kg
Zebra	200 kg	Warthog	45 kg
Topi	100 kg	Giraffe	750 kg
Thomson Gazelle	15 kg	Kongoni	125 kg
Grant's Gazelle	40 kg	Eland	340 kg
Buffalo	450 kg	Waterbuck	160 kg
Cattle	180 kg	Shoat	23 kg

Statistical Analysis

Biomass estimates from randomly located plots measured during both the long and short-grass seasons, were tested against distance from the river (the relative location on the catena). A Student-Newman-Keuls (SNK) analysis of variance was applied to the biomass estimates pooled for both 0.5 and 1.0 km incremental distances from the river. A Pearson correlation between distance and biomass was applied to pooled (both seasons) data. Long and short-grass biomass estimates were tested for significant difference with a simple *t*-test.

The percent of range found within shortgrass condition during 1981 and 1982 long-grass seasons, with respect to distance from the river, was tested between the years using a paired *t*-test.

Analysis of the influence of catena on herbivore biomass (excluding hippopotami) was accomplished through

analysis of variance. The influence of season, based on recorded rainfall pattern, was similarly investigated. A second analysis was performed excluding species not exhibiting significant seasonal movements, as determined through analysis of variance, as well as species not sighted on more than 30 occasions.

Cumulative herbivore biomass was calculated for catena by month for each species included in the census. Rates of forage offtake were calculated per species by month and catena. Daily dry forage requirements for ruminants were calculated according to the equation: $X=0.09(\text{body weight})^{75}$, and requirements for monogastric herbivores (warthog and zebra): $X=0.11(\text{body weight})^{75}$ based on metabolic body weights per species (R. Hudson, Univ. of Alberta, pers. comm.). The daily requirements of the average sized hippopotamus is approximately 18 kg (dry weight) of grass per day (Laws 1963, Field 1970).

Results and Discussion

Seasonal Grass Biomass

The standing dry biomass of grass (Fig. V.1) within a 3 km radius of the river increased 61% between the short-grass season (data collected in mid January 1982) and the long-grass season (late June 1982). These results, obtained by the horizontal intercept method, compare favourably with maximum and minumum mean monthly cliplot biomass records. A

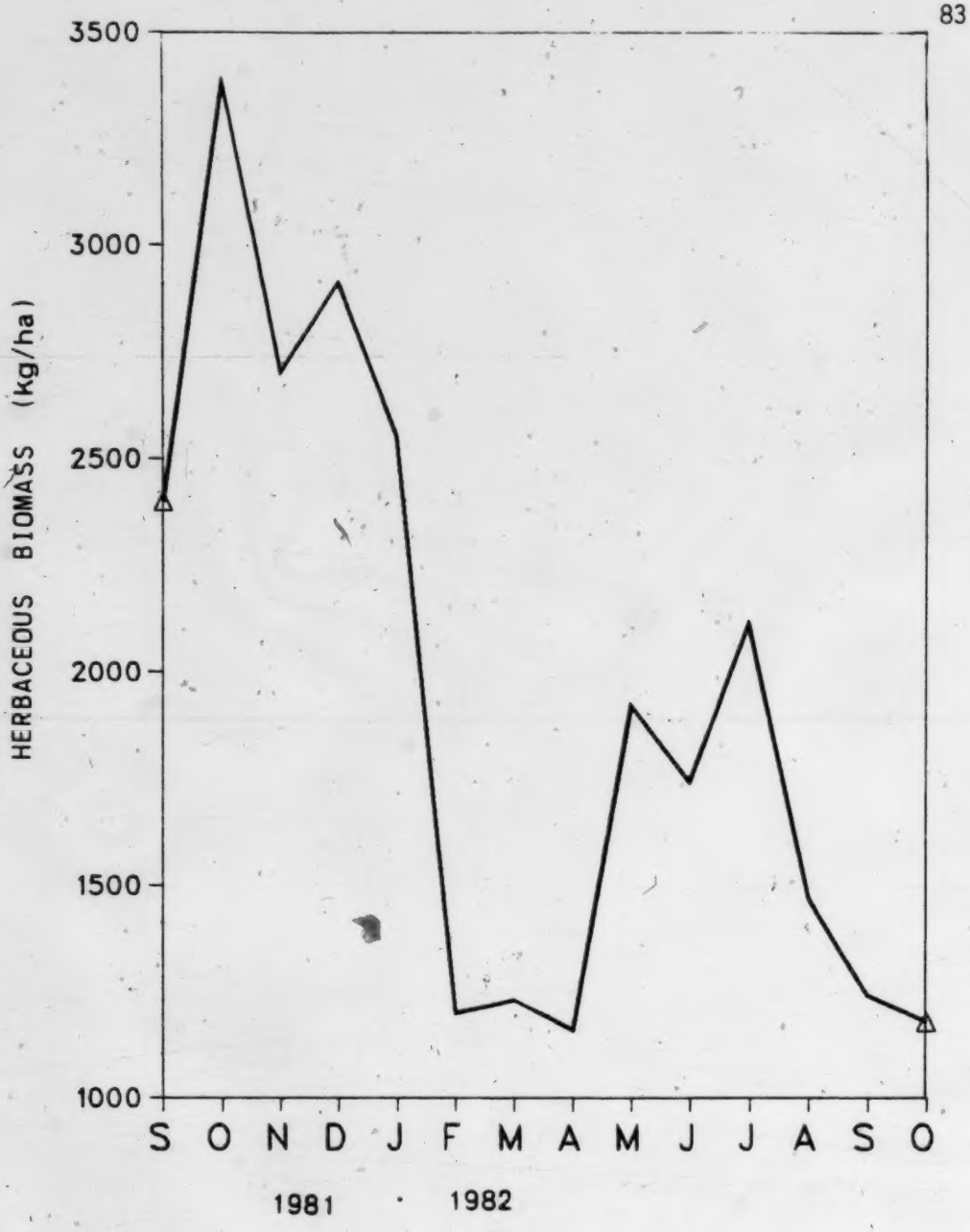

Figure V.1 Estimated monthly herbaceous biomass (kg/ha) averaged from riverine plots. Data were collected from Sept. 1981 to Oct. 1982 along the Mara River.

decrease of 65% was recorded between the 1981 long-grass period (October) and February 1982. The clip plot records probably do not accurately reflect total range condition, as all were collected within 50 m of the Mara River. Appendix 3 presents the tabled data and a description of the techinque.

Biomass estimates from the randomly located (seasonal) plots revealed significant negative correlations between biomass and distance from the river, for the eastern side of the Mara River, for both the long ($P<.01$) and short-grass ($P<.1$) seasons. The western side of the river revealed a similar relationship between standing biomass and distance ($P<.1$) for short-grass data, though not for long-grass data. A Pearson correlation applied to pooled data revealed a small though highly significant correlation existed between weight and distance ($r=-.28$, $p=.005$).

The 1 km catena divisions investigated through the SNK analysis of variance proved generally non significant for standing grass biomass. Mean values for each catena during the long-grass season were 1860 kg/ha for the low catena, 1770 kg/ha for the middle, and 1050 kg/ha for the high catena. The mean dry weight of grass for the long-grass season was 1670 kg/ha. Short-grass sample results were means of 1320 for low, 860 for the middle, and 1060 kg/ha for the high catena, with an overall mean of 1040 kg/ha. Long-grass measurements were taken during the 1982 season, which was markedly less productive (due to less rain) than the 1981 season.

The presence of highly productive ox-bow marshes and associated low areas along the river may account, in part, for the gradient in forage availability observed with distance from the river. Another factor, the relatively low utilization of the riverine catena by ungulates, allows for a greater carryover of wet season grass production into the dry season. The observed gradient in forage availability, with respect to distance from the river, is evidently due both to higher productivity due to drainage, and the low herbivore biomass within the riverine catena. In addition, intermediate levels of grazing may stimulate a higher level of grass productivity (Sinclair and Norton-Griffiths 1979).

Distribution of Grazed Areas

Analysis of the amount of range maintained within short-grass condition during the 1981 and 1982 long-grass seasons proved significantly different between years (*t*-test, $P<.05$). The percent of range maintained as short-grass 'lawns' for the 6 km of transects studied (Fig. V.2), increased from 41 to 60% between the 1981 and 1982 long-grass seasons. This reflects the temporal distribution of precipitation for the area for the two years. During April, May and June, the wet season, 453 mm of rain was recorded in 1981, 342 mm in 1982.

Rainfall records are incomplete for 1982, though comparing cumulative rainfall for the months January through September, 863 mm fell during this period in 1981; 734 mm in

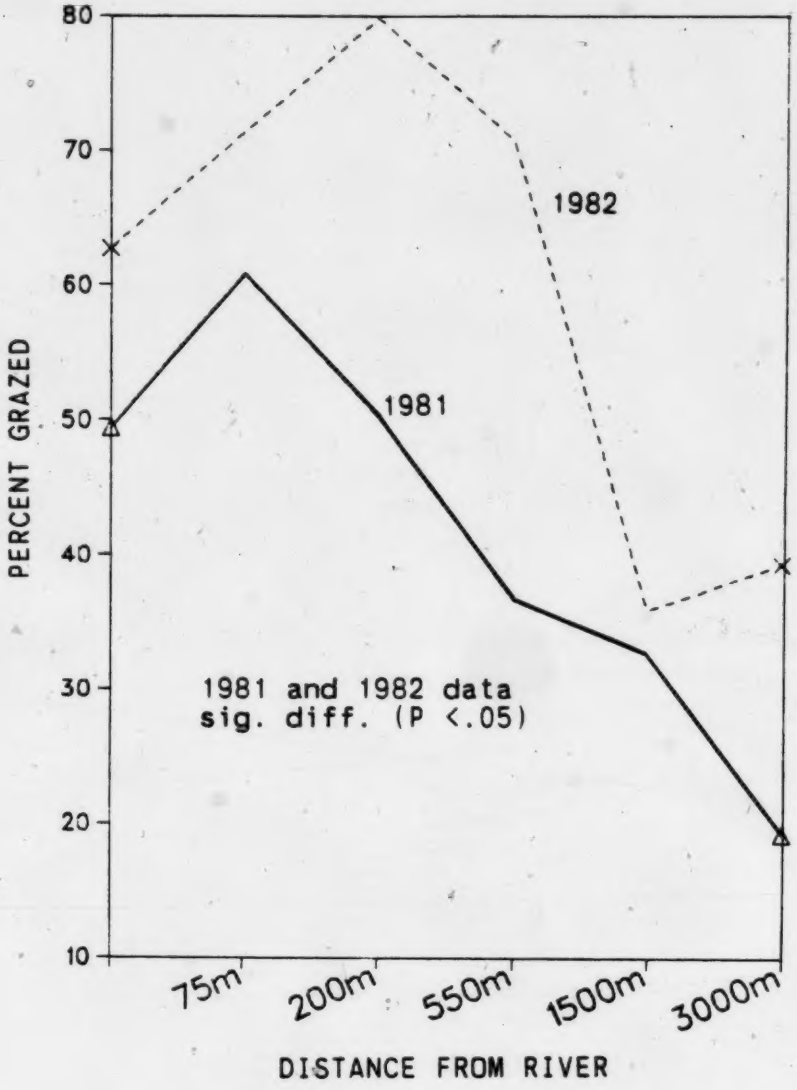

Figure V.2 Result of transects along the Mara River to determine to proportion of grassland maintained in short grass condition by grazing herbivores during the 1981 and 1982 long grass seasons. The X axis is a rounded logarithmic progression.

1982. The difference in rainfall is reflected in the amount of long-grass maintained within short-grass condition.

The proportion of grassland within the short-grass state during the long-grass season reflects the amount of grazing area available to hippopotami at this time. Long-grass is grazed infrequently by hippopotami (Field 1970, Mackie 1976), and the grazing mosaic must be established at the onset of the wet season. If grass growth is rapid, lawn area would conceivably be restricted both by lowered requirements in terms of area, for hippopotami, and a higher proportion of the range 'getting away' into the long-grass state. The influence of other herbivores on the shared range can be left to conjecture. Obviously, the migratory species, wildebeest and zebra in particular, have a tremendous effect upon grass height and standing biomass, though this is not evident until early in the dry season. Fire, primarily set by pastoralists, also releases large areas of range from the long grass state, begining early in the dry season.

There was no evidence of forage limitation for hippopotami during the long-grass season. The only noticeable difference between years, as a result of the proportion of range available as lawns, was that during the lush 1981 wet season, hippopotamus paths were more heavily travelled and extended further from the river. The mid and upper catenas contained higher proportions of short-grass (Fig. V.2). Observations indicated that lawns within the low

catena were maintained primarily, if not exclusively, by hippopotami.

Though movements of hippopotami at night were not recorded, path extents and orientations provided evidence of habitat use. Feces and tracks, as well as the unique swath-like grazing patterns within short-grass range, provided an accurate and relatively objective impression of preferred habitat and foraging distance from the river. My observations are in accordance with Laws (1963) estimate of 3.2 km as the average maximum distance from water travelled during foraging.

The upper catenas supported a much larger population of herbivores during the long-grass season, particularly animals usually associated with short-grass, such as Thomson's and Grant's gazelle. I suspect that a shared benefit, realized through the maintenance of extensive areas of short-grass, is gained for all species utilizing these areas during the wet season.

Ungulate Populations

Results of a two-way analysis of variance for ungulate biomass by season (based on recorded rainfall), catena, and season by catena, were significant ($P<.05$). The same analysis by month, instead of season, was also significant ($P<.05$). The specificity in spatial and temporal occupancy of the range by herbivores may be due to several factors such as plant species zonation (trees in particular),

resource partitioning and predator or insect avoidance. Most of these factors could also be considered to exibit some form of seasonal cycle.

Mean monthly ungulate biomasses for the low, middle, and high catenas were 95.4, 195.6, and 146.5 kg/ha respectively (Fig. V.3). Average monthly biomass over the three catenas was 146.5 kg/ha. This is substantially higher than records from the Serengeti for 1965 of 57.0 kg/ha (Pratt and Gwynne 1977), though less than estimates for the Mara plains; 236.0 kg/ha (Stelfox *et al.* (1980). Appendix 4 presents data for animal species, numbers observed, and distribution by catena and date.

Identification of resident and transitory species was accomplished through a one-way analysis of variance; month by species. Animals determined to be resident ($P>.05$) were buffalo, waterbuck, impala, kongoni, eland, and cattle. Warthog is considered a locally resident animal (Eltringham 1974), though the analysis revealed a significant monthly fluctuation in number ($P<.05$). This is probably due to an increase in sightings shortly after the young emerge from dens in September, followed by a decrease due to high mortality amongst young during the first few months. Tall grass also lowers count efficiency for warthog, and the species, unlike another small animal, the Thomson's gazelle, does not appear to avoid areas of tall grass. Visibility error was not considered significant for other species.

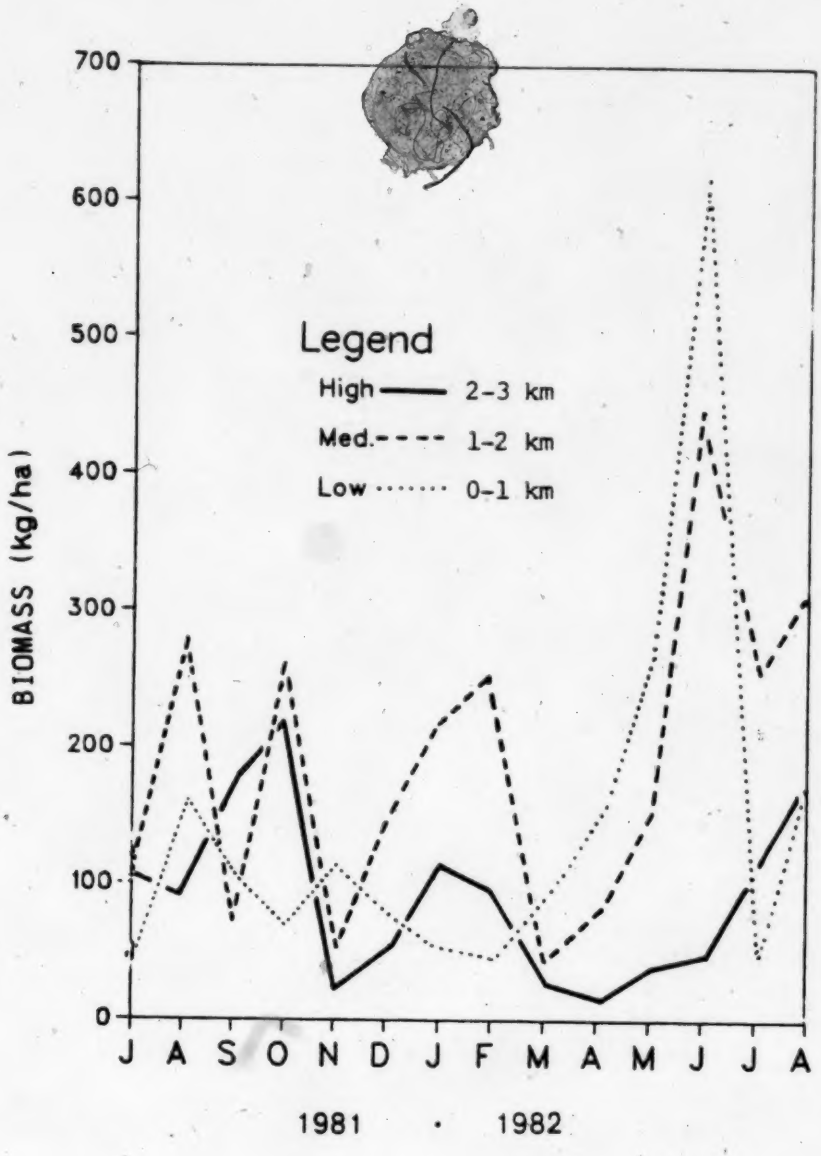

Figure V.3 The estimated average monthly biomass of major grazing herbivores and their distribution among three catena levels extending from the Mara River. Data are from weekly censuses taken along the 10 km study section, from Jul. 1981 through Aug. 1982.

Rangeland Productivity and Offtakes

Rainfall, recorded for the study area, is presented in cumulative monthly totals in Fig. V.4. Precipitation is the primary determinant of vegetative growth, and hence, animal occupancy of grassland. This is illustrated in the relationship between rainfall and the estimated monthly (dry weight) grass offtakes for the study area (Fig. V.5). Figs. V.6 and V.7 present the proportional monthly offtakes by wildebeest and zebra, the major migratory species.

The occupancy of the 10 km stretch of Mara River adjacent to the study area ranged from a low in June 1982 of 17.1 hippopotami/km to 30.3/km during February 1981, responding to subsiding river levels during the dry season. This section of river contained a higher number of low-water pool sites than the adjacent up or downstream stretches of the same length. This resulted in an increase in hippopotami within the study section during the dry season, when river levels were low. Increased grass offtakes were evidenced as hippopotamus numbers rose (Fig. V.5). The January - April 1982 period witnessed consistently high hippopotamus numbers and grass biomass offtakes.

Dry weight grass offtakes by hippopotami, in relation to total animal offtake (giraffe, a browser, is not included), ranged from 8% in June 1982, to 46% in March 1982. Cumulative monthly consumption of grass (dry weight) by hippopotami ranged from 32 kg/ha during June 1982 to 55 kg/ha in February 1982.

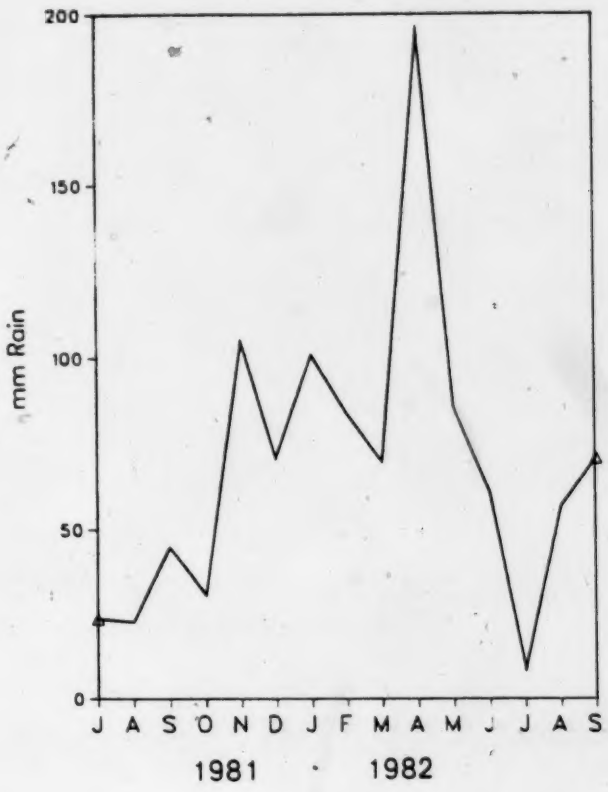

Figure V.4 Monthly precipitation records for the Mara River study section from Jul. 1981 through Sept. 1982.

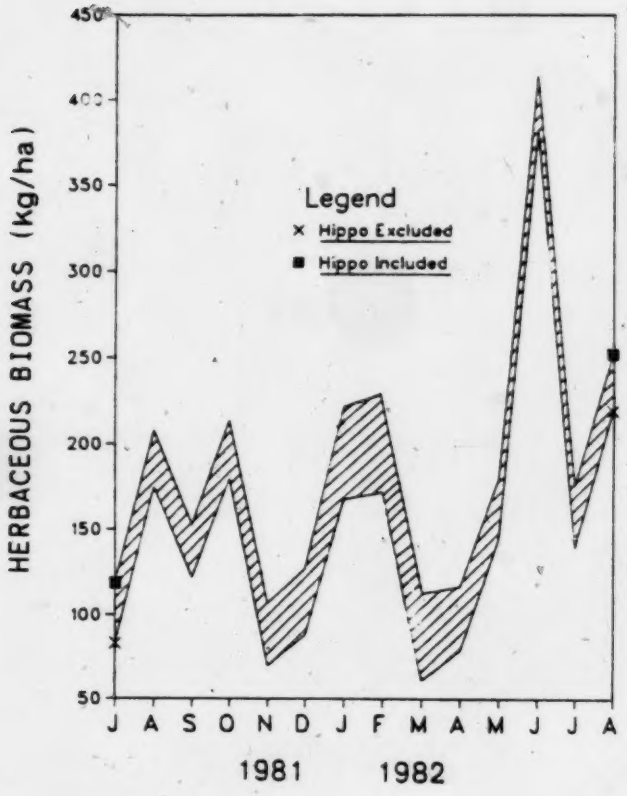

Figure V.5 Estimated monthly grassland herbaceous offtakes for the major grazing herbivores, based on the weekly census along the Mara River study section (lower curve), with estimated hippopotami offtakes shown as an added increment (shaded area). Total offtakes are represented by the upper curve.

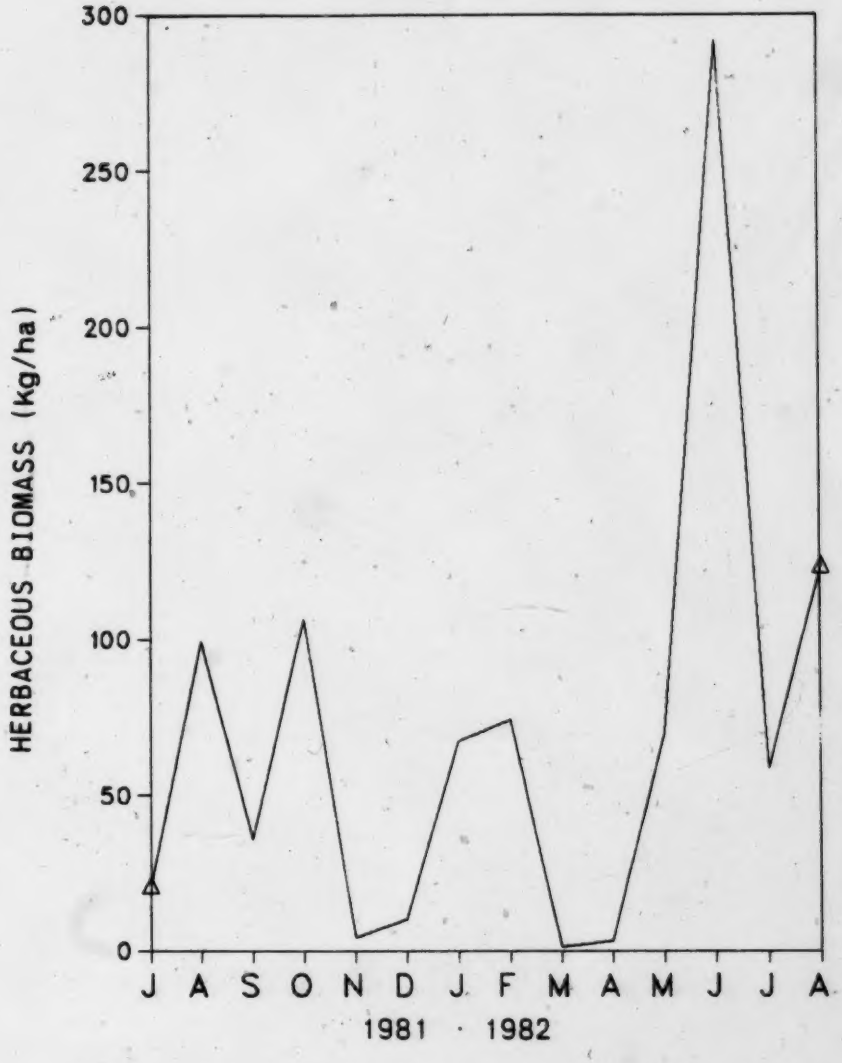

Figure V.6 Estimated monthly grassland herbaceous offtakes by wildebeest, based on the weekly census along the Mara River study section, from Jul. 1981 through Aug. 1982.

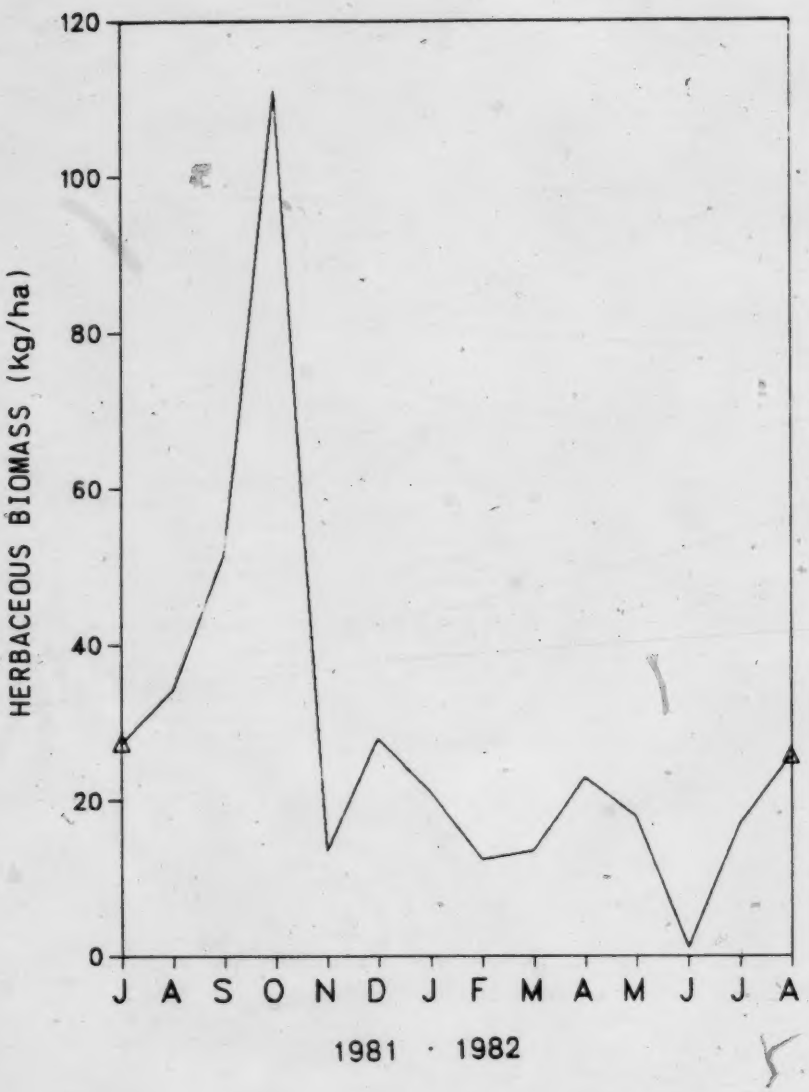

Figure V.7 Estimated monthly grassland herbaceous offtakes by zebra, based on the weekly census along the Mara River study section from Jul. 1981 through Aug. 1982.

Due to the dry season distribution of hippopotami along the Mara River, with higher pool occupancies during low water levels, forage removal by hippopotami was more spatially heterogenous during the dry season. This resulted in the most intense period of grazing pressures within the study area occurring during the period of lowest grass productivity, and occuring in the vicinity of several high density pools.

Sinclair and Norton-Griffiths (1979) provide a regression equation based on mean monthly dry season rainfall (July - October) that predicts dry season grass production for the Serengeti. Since the Mara and Serengeti are considered within the same major ecosystem, this equation can be used to predict dry season production for the study area.

During 1982, the mean monthly rainfall was 42 mm. Estimated grass production is 3.61 kg/ha/day. This represents the green growth that is selected by hippopotami. Requirements for hippopotamus alone, at peak occupancy for the study area (30 hippo/km of river), was 0.91 kg/ha/day, or 25.2% of dry season daily production.

A simple partitioning of dry season range productivity between hippopotami and the other herbivores during the dry season, reduced the amount of forage available to hippopotami to below estimated daily requirements. If hippopotamus grazing does not actively exclude other herbivores, and the other herbivores extend the time spent

grazing in order to meet daily intake requirements, only 75% of the estimated daily requirements of the study area's hippopotami would be met. At no time were hippopotami observed to extend grazing times into daylight hours.

The above estimates are conservative, the actual densities of hippopotami/ha of rangeland are not directly proportional to densities/km of river due to the compression of river distance caused by meander. This may account for a 20 to 30% decrease in available rangeland per km of river, dependent on the amount of convolution exhibited by the river channel.

Fires (estimated over 60% of the study area in 1981, 25% in 1982), and the massive short term forage removal from the annual wildebeest migration,can conceivably reduce the long-grass carryover into the dry season to negligable levels. Though hippopotami do not rely heavily on seasonal forage carryover, a lack of carryover would place more pressure on dry season production, or 'greenflush', and hence increase intra-specific competition during the dry season. This situation apparently did not arise during this study, as hippopotami, evidenced by spoor and the typical swath-like freshly grazed areas, had nearly sole possession of productive ox-bow marshes and associated low areas close to the river.

Offtakes attributable to herbivores not counted in censuses may be considerable, and exhibit strong seasonality. Insects in particular, such as grasshoppers,

locusts, and army worms, have the potential to denude large areas of vegetation. The number of army worm found during a short, localized infestation within the study area during 1982, were 92, 210, and 3 within 3 respective 1 m^2 clip plots. Hot dry weather apparently imposed a premature end to the infestation.

Estimates of dry season productivity provide an insight into range carrying capacities during extended dry periods. Though it is difficult to predict stocking rates for the study area during drought, it can be expected that there would be significant pressures exerted on the range by animals relying on the river for water. Under such conditions it is improbable that, at the densities recorded during this study, hippopotami would be able to meet their daily forage requirements.

Several factors benefit hippopotami through dependence upon the river as the focus of foraging radius. During the study, forage biomass was highest closest to the river, and the low catena experienced the lowest ungulate stocking rates and forage offtakes.

There is strong evidence that the maintainance of hippopotamus grazing lawns results in increased productivity within these areas (Sinclair and Norton-Griffiths 1979). This, plus the species apparent ability to withstand long periods of food shortages by relying on metabolic reserves (Pienaar *et al.* 1966, Vesey-Fitzgerald 1960) tends to counterbalance, to a degree, the range restrictions imposed

through a specific day-habitat.

During the period of this study there was no evidence that the hippopotamus population within the Mara River was experiencing environmental stress. No signs of undernourishment were noted during the dry season, and providing the rainfall regime remains constant, I feel this hippopotamus population has the potential to double its present size before suffering significant forage limitations. Data reveal that during 1981 and 1982, there were only three months when herbaceous productivity fell below the daily requirements of hippopotami (based on a partitioned resource amongst grazing herbivores within 3 km of the river). Forage carryover from wet season productivity could be used as a sub-optimal diet during the driest months, and the patchiness of the riverine habitat provided year-round, though limited, areas of preferred forage. Range condition would likely suffer a downward trend before forage limitations become apparent for hippopotami, a process recorded for other hippopotamus populations (Thornton 1971, Lock 1972).

Carrying capacity though, does not simply rest with how much food is available to a population. Many factors, most of which are complexly interdependent, all combine to determine how many animals, and of what type, a given area of land can support. The Mara-Serengeti ecosystem is evolutionarily old and highly developed, as evidence by it's rich variety of species and complex system of resource

partitioning. The influence of a mega-herbivore, the hippopotamus, is an important consideration, especially when the population is increasing while others, such as the wildebeest, have apparently stabilized (A. Sinclair, Univ. British Columbia, pers. comm.).

ENVIRONMENTAL IMPACTS

Introduction

In many parts of Africa, attention has been drawn to hippopotami as a result of their ability to modify rangeland ecologies. Most published literature dealing with density-dependent environmental impacts of hippopotami comes from investigations near the Kazinga Channel, Uganda, where overstocking caused extensive damage to areas close to water. In and around the Mara River, large-scale detrimental effects upon the ecology were not in evidence, though the stability of the local ecology was in question in light of the high density hippopotamus population.

Spinage (1958) and Bere (1959) identify a 'problem' based on overgrazing and erosion, plus the large number and poor physical condition of hippopotami in the Kazinga area. Reduction of the population began in 1958 with the complete elimination of hippopotami from the Mweya peninsula, approximately 11.4 km^2 in area (Bere 1959). The exclusion program continued until 1968 (Eltringham 1974) and provided the setting for the classical removal experiments made into the area's grassland ecology (Eltringham 1974, Lock 1972), and herbivore populations (Thornton 1971). Both the grassland and animal components showed marked responses to the exclusion of hippopotami.

The hippo's method of grazing, grasping grasses between wide horny lips and pulling off with a sideways swing of the

head, often uproots grasses. Soil exposed in this manner and subsequently trampled, is subject to erosion. Sheet erosion is most common in this situation (Lock 1972, Olivier and Laurie 1974). For this reason, low lying stoloniferous and rhizomatous grasses such as *Chrysochloa* and *Sporabolus*, often become dominant within grazing mosaics (Thornton 1971, Lock 1972).

Erosion and related habitat degradation have been the major factors drawing attention to high density hippopotamus populations. The most visible and permanent effect is the erosion of topsoil that has taken decades if not centuries to accumulate. Thornton (1971) notes large areas where the top 3 to 8 centimeters of sandy loam has been washed away, exposing a clay hardpan. Lock (1972), also on the Mweya peninsula, investigated the effects of trampling, finding soil compaction significantly different between open areas and under bush clumps; 48% and 64% pore space respectively for the top 5 cm. Lock (*op. cit.*) noted that the activities of earthworms were reduced or anulled by trampling, further decreasing soil pore space. Thornton (1971) described trampling leading to severe compaction; soils possessing a "plate-like non friable structure" severely restricting grass regeneration. In addition, the lack of litter on eroded soil surfaces combines with compaction to limit rain water infusion (Thornton 1971, Lock 1972).

Pathways to water created and maintained by hippopotami form natural drainage courses for surface runoff. As erosion

progresses, the V-shaped cut commonly increases in steepness. Thornton (1971) measured and staked one of the larger gulleys thought to have been created by the activities of hippopotami and measured an inland extension of 7 m between May 1958 and May 1962.

Along with soil losses to water are losses of nutrients, particularly when topsoil is eroded. The dunging behaviour of the hippopotamus results in the greater proportion of feces excreted into the river. This results in a massive loss of nutrients from the land to the water, and very little of this could conceivably be returned to the land.

This chapter addresses the apparent impacts upon the riparian environment that the Mara River hippopotamus population has exhibited, including vegetation and soils, specifically; plant basal cover, amounts of litter and the cause and effects of riverbank erosion. Some human/hippopotamus interactions and conflicts are described, the major problem area being crop depredation.

Major detrimental impacts upon the riparian ecology of the Mara River were not evidenced during the course of this study (June 1981 - October 1982). The presence of hippopotami within the riverine rangeland promotes increased productivity of grasses in response to grazing, and suggests the maintenance of a zootic-disclimax seral state benefitting many other herbivores in addition to hippopotami.

Methods

Range Condition

During the 1981 long-grass season, the amounts of bare earth and litter on the ground were recorded for 28 sites. A 1 m rod graduated at 2 cm intervals was used as a point-intercept line in order to record the presence of litter and bare earth at 50 points for each site. A grazed area ('lawn') was measured, as well as the center of the closest adjacent area of tall grass.

T-tests were applied to data in order to ascertain whether significant differences were evident in the amounts of bare earth and litter between the short and long-grass components of the mosaic.

Seasonal Dynamics of Grazing Mosaics

Four transects recording the exact position of hippopotamus grazing mosaics, were located through areas proximal to the river. The sharp demarkation between long and short-grass, plus swath-like grazing patterns, identified the mosaics to be established and maintained by hippopotami. Each transect was measured in June during 1981 and 1982 at the height of the long-grass season. This procedure determined whether individual mosaics were reestablished at the onset of each long-grass season. The mosaic pattern is not discernable during short-grass conditions.

Riverbank Degradation

Exit/entrance paths were staked from June through August 1981 and remeasured one year later. Paths used primarily by hippopotami were identified by their typical flat-bottomed U-shaped cross-sectional configuration. Other animals, particularly buffalo and waterbuck were observed to use the paths on occasion, though apparently not enough to contribute significantly to establishment and maintenance. Most ungulates water at large pan-like approaches to the river in order to reduce predation. A simple clinometer was used to record path gradient during remeasurements.

The majority of runs were staked along 300 to 500 m stretches of riverbank within a 10 km section of river adjacent to the field camp. No specific selection was involved, other than indications of recent use. In addition to individual run measurements, runs were counted along both banks of the river over a 6.8 km section in order to determine the average number of runs per unit length of river.

Results and Discussion

Seasonal Dynamics of Grazing Mosaics

Individual lawn locations for the 1981 and 1982 long-grass seasons are represented, for two transects, in Fig. VI.1. Two of the four transects recorded in 1981 were within areas of homogenous short-grass in 1982, and are not

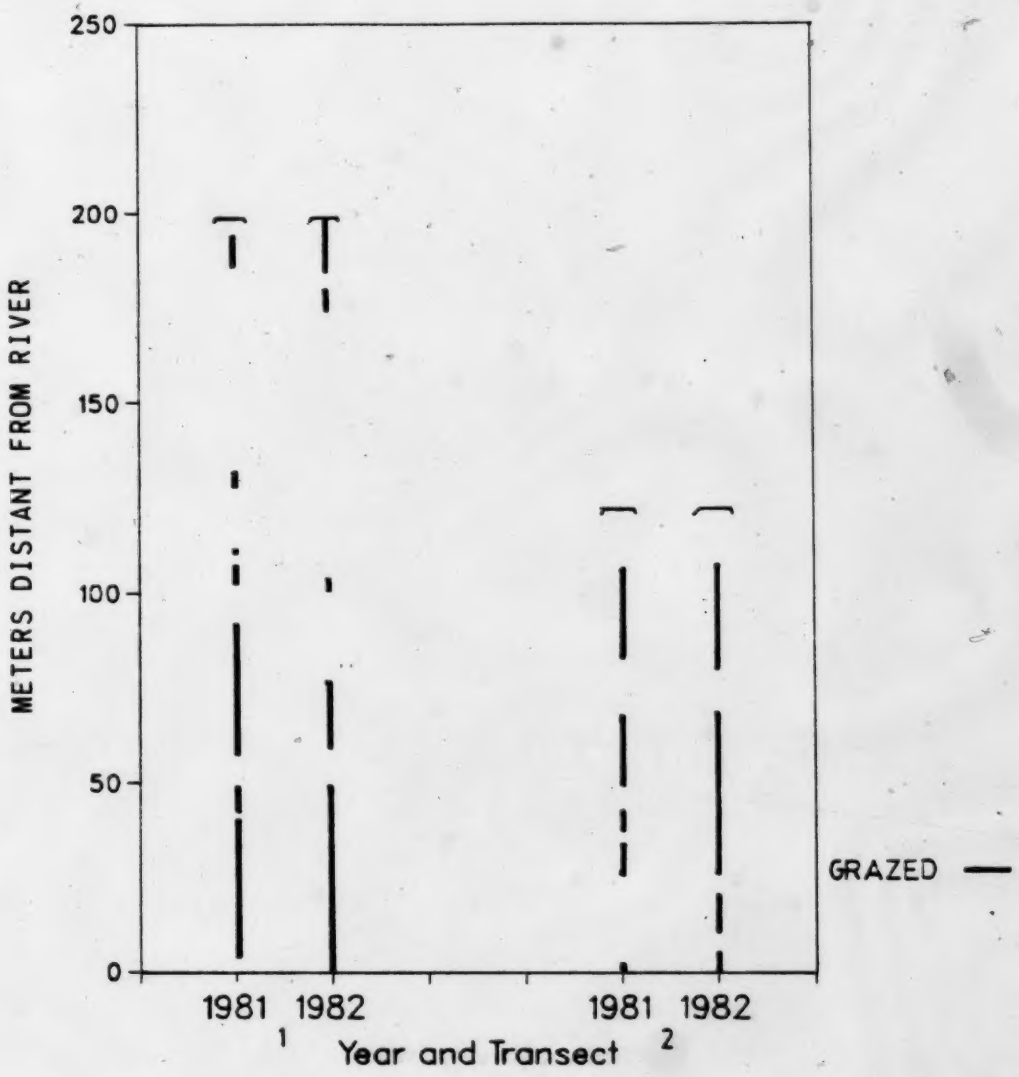

Figure VI.1 Hippopotamus grazing mosaic locations recorded for two transects located along the Mara River study section. Measurements were made during the 1981 and 1982 long grass seasons.

presented.

The two transects successfully remeasured in 1982 revealed that there may be specific site selection for the establishment and maintenance of lawns. Qualitative or quantitative differences between mosaic components must be apparent to hippopotami as the intervening short-grass season obliterates any visual evidence of lawn location between long-grass seasons. Reestablishment of lawns at specific locations may lead to succession in plant species composition and erosion of valuable topsoil. Terrace erosion, a distinctive feature of short-grass hippopotamus 'lawns' subject to constant use, has been noted by Bere (1959), Thornton (1971) Lock (1972) and Olivier and Laurie (1974). Runoff water passing over the short-grass lawn, creates an undercut ridge at the border with tall grasses. This is because the roots of the ungrazed grass bind the soil more tightly and are more numerous than those of the overgrazed trampled lawn. Much soil may be lost to the river (Olivier and Laurie 1974). Only very localized surface erosion was evident within the study area, due primarily not to light stocking rates, but to the favourable rainfall regime (Sinclair and Norton-Griffiths 1979). High grass productivity and extended growing seasons, provided a greater resistance to surface erosion resulting from trampling and overgrazing.

Grazing-related succession has been investigated in previous work (Scotcher *et al.* 1978, Lock 1972, Thornton

1971) and has been shown to alter species composition, as well as contributing to soil compaction and erosion. The evidence of succession is most strongly shown in Thornton (1971), Lock (1972) and Yoaciel (1981), the authors noting an immediate improvement in plant cover and increases in litter and soil porosity resulting from hippopotamus exclusion, contributing to a more acceptable substrate for a wider variety of grasses. Yoaciel's (1981) work compares herbivore biomass on the Mweya Peninsula and successional impacts on the grass community between 1954-1961 and 1964-1975. He concludes that the habitat deterioration evidenced during the 1950's was primarily due to low rainfall. Lock (1972) notes that the predominance of *Sporabolus* under high grazing pressure may be due to a lack of competition from taller species, which lose flower and seed stock to grazers. Although range erosion was not apparent within the study area, the re-use by hippopotami of roughly the same locations from year to year, focusses impacts on specific sites.

Bare Earth and Litter Within the Grazing Mosaic

A significant difference (P=.009) in the amount of litter between the long and short-grass components of the hippopotamus grazing mosaic, was revealed by *t*-test results. Less litter was recorded within grazed areas. Amounts of bare earth, an indication of percent plant basal area, did not reveal a significant difference between long and

short-grass areas. Hence, there appears to be no serious long-term impact on productivity, and the successional state maintained through consistent offtakes by hippopotami may improve the value of the range to other grazers.

Eltringham (1974) and Lock (1972)showed that grasslands heavily used by hippopotami exhibited a marked increases in the proportion of bare earth. They mention that a natural response to persistant grazing pressure is the increased dominance of low lying stomaceous and rhizomatous grasses. These grasses, such as *Chloris guyana* and several species of the *Sporabolus* genus, increase total basal cover by producing a mat-like ground cover. Along the Mara River, these species are particularly in evidence within the first 100 m distant from the river, indicating a similar response to grazing.

Soil compaction, as a result of trampling by hippopotami, tends to exclude even low lying species (Eltringham 1974, Lock 1972). Evidently, either edaphic qualities of the soil along the study section of river resist compaction and the related plant succession, or the intensity of use by hippopotami within grazing mosaics is not sufficient to compact soils to the point of reducing plant basal area significantly. I believe the latter is most probable.

Fire Exclusion and Woody Vegetation Regeneration

The large quantity of grass biomass removed from rangelands by high density hippopotamus populations is associated with reductions in extent and intensity of range fires within the riverine habitat (Dodds and Patton 1968, Olivier and Laurie 1974). The long term consequence is an expansion of woody vegetation (forest and/or thicket associations). Dodds and Patton (1968) attribute the almost complete disappearance of hippopotami from the Lukusuzi River, in Zambia, to a reduction in forage range resulting from increased mopane thicket.

Range fires reduce woody regeneration by burning back small plants (less than 1.7 m in height) to rootstock (Olivier and Laurie 1974). Browsing herbivores, such as elephant and giraffe, may also play a large role in controlling the areal extent of woodland. Separating the various influencing factors is difficult, though evidence of overall trend may be gained in a number of ways, such as monitoring vegetation cover changes over time via aerial imagery, and assessing rates of regeneration/destruction on the ground.

Analysis of the dynamic state of the Mara River woody vegetation was not made during this study, though it has exhibited a decreasing trend within the Masai Mara National Reserve over the past decade (E. Trump, Wildlife Planning Unit, pers. comm.). Examination of ungulate biomass distributions within catenas by month (Chap. 4, Fig. 4.3)

revealed that few ungulates utilize the riverine catena (containing most of the riverine woodland) during the first two thirds of the long-grass season. During this period, hippopotami traveled further inland to graze, as evidenced by path extension and use. Rangeland within the upper levels of the catena, outside the riverine woodlands, are more heavily grazed by all herbivores.

Major fuel reductions within the riverine woodland caused by hippopotamus grazing were not evidenced during this study. The converse was apparent, and during 1982, when only 25% of the range was burnt, fires were more frequent within the riverine catena than within either medium or high catenas. Forage offtakes during this period did not serve to exclude fire from the wooded areas. The reduction of woody vegetation along the Mara River seems the result of high grassland productivity, providing fuel for range fires and reducing regeneration. The effect of hippopotamus grazing is minimal.

Riverbank Degradation

Soil removal from the leading edges of entrance/exit paths incised into the riverbank averaged 0.53 m^3/yr (N=63, S.E.=.072). Along 8 km of river, 305 paths exhibiting signs of current use were counted; 45 paths/km of river (both banks). This computes to 23.6 m^3 of earth eroded per year from the inland progression of paths. Total path erosion is far in excess of this, some paths extending more than 10 m

from end to end.

Not only the riverbank, but the channels of seasonal watercourses undergo bank degradation resulting from hippopotamus activity. The use of drainage channels as primary exits, with paths radiating from the channel bed serve to concentrate impacts over small areas.

Initial path establishment seems to be commonly the result of hippopotami sliding down nearly vertical banks, up to 5 m high. Skid marks down steep runs were noticed after rains and several times spoor was observed only part way up muddy paths, evidence of a hippopotamus unsuccessfully attempting egress.

Placement of paths, often at depressions along the bank, can form extensions of natural surface drainage. The path then can be largely shaped by runoff erosion. Path gradient is, on the average, quite steep; 21.2 degrees (range= 11-48 degrees, N=63, S.E.=1.16). Observations indicate that paths acting as runnoff channels typically become steep and undercut at the leading edge and no longer passable by hippopotami. It is common to see two or three new paths established alongside such a runnoff channel, an observation also made by Olivier and Laurie (1974). More efficient surface drainage reduces amounts of water absorbed by soil. This may be of particular importance during the dry season, when most rainfall is of very short duration and maximum adsorption is necessary to provide a perennial plant 'greenflush'.

An average of 8.7 abandoned paths per kilometer of river were counted. The evident cause of abandonment for the majority of paths was unacceptable steepness or width (too narrow), resulting from runoff. Slumping of the riverbank and root obstructions were noted, though less commonly.

Hippopotami use their thick lower incisors to gouge mineral laden soil. Like the elephant, hippopotami have the ability to break up compacted soil using their teeth. The 'licks' are often the exposed vertical bank of the river at or slightly above the waterline. Hippopotami do not leave the water while gouging at the bank for soil, and cause large, sometimes 1.5 m deep, undercuts into the bank. Resultant slumps of the riverbank always occur at these spots, and over time channel configuration can be markedly altered.

Five actively maintained riverbank licks were noted along 10 km of river. Inland, areas of water upwelling during the wet season provided mineral laden soils for all species, hippopotamus included.

Human/Hippopotamus Interactions

During the past 5 years, several extensive wheat and maize farms have been developed within the Mara-Narok region. One farm, established partly on the lowlands adjacent to the Mara River in 1980, has proven that the immediate area of this research project is acceptable for cultivation, at least under the present favourable rainfall

regime. Masai group ranch lands are leased to farmers with the necessary capital and equipment for large-scale farming.

Crop depredation by wildlife, hippopotami included, seems to be effectively controlled by electric fencing. Migratory wildebeest prove most problematic in breaking down fences (W. Roberts, Mara area farmer, pers. comm.).

Shooting, in response to crop depredation has been carried out by authorities during 1982, with one unit of rangers from the Kenya Wildlife Conservation and Management Department stationed at Emarti village (at the north end of the 127 km census stretch), most actively involved. Several hippopotami, the exact number not determined, were shot during August and September 1982.

Cash crop smallholdings along the Mara River are not enclosed by electric fencing and are mainly situated on the fertile lowlands adjacent to the river within the grazing range of hippopotami. There are few alternatives to fencing, short of eliminating the local population, that will effectively exclude hippopotami from gardens.

Hippopotamus numbers north of the Reserve increased dramatically between 1980 and 1982. This, combined with increased population and agricultural pressures exerted by the human residents in the area, will undoubtably result in an appreciable conflict between human interests and the hippopotamus population within the Mara River. The establishment of group ranches for the traditionally nomadic Masai has provided an alternative to a purely pastoralist

lifestyle. The amount of land leased to wheat and maize farming, and the interest exhibited by the Masai in farming, was increasing. In addition, with increasing populations amongst the tribes within the Mara-Narok area, tribal boundaries have become more clearly defined. Movement of livestock across these borders has become less acceptable, limiting the available hetrogeneity of grasslands for grazing.

Masai did not feel that hippopotami within the Mara River were a threat to livestock production. Appendix 5 provides the results of a short questionaire concerning Masai attitudes toward the hippopotamus population.

The latter part of 1982 evidenced a large influx of cattle, sheep and goats into the study area, an increase over previous months of close to 200%. This was in response to low rainfall in the surrounding areas. The focussing of grazing pressures by livestock in this manner can result in greatly increased forage competition between livestock and hippopotami.

The potential for increased friction between humans and the hippopotamus population within the Mara River exists. Both pastoralists and agriculturalists along the river can be affected, and in some cases already are. Problem identification and resultant action is simpler and more effective in response to hippopotamus/crop conflicts. The reduction of available grazing range for hippopotami has the potential to compound problems such as crop depredation.

Less obvious are the indirect conflicts resulting from impacts upon the grassland ecology. That the carrying capacity of grassland adjacent to the river for livestock is in part determined by hippopotamus grazing pressures is obvious. The long term environmental impacts of a high density hippopotamus population may be accelelerated by the presence of large numbers of livestock. For example, sheep and goats, with their ability to crop grasses close to the ground, may select for grazing within the short-grass lawns established by hippopotami. This would serve to further reduce plant basal cover and increase surface soil erosion.

During the dry season, the dependence of livestock upon the river for water is absolute within the study area. I feel that increased biomass for both livestock and hippopotami along the Mara River will result in increased environmental stress. Plant community succession may be reversable once impacts lessen, but the loss of topsoil to surface erosion and the increase in surface water runnoff has long term repercussions.

SUMMARY AND CONCLUSIONS

This study has fulfilled most of it's initial objectives, though the near-optimal environmental conditions experienced during the field program did not impose stresses that would undoubtably have provided a greater insight into the mechanisms of the ecology of the Mara River hippopotamus population. Census results defined the growth and status of the population, as well as accurately recording distributions valuable in assessing habitat preferences. Habitat associations must be interpreted as representative of an unstressed state. Selectivity may shift from a pool to a forage resource focus under conditions of forage limitation. Similarly, the relatively small role that social parameters played in the regulation of population growth cannot be considered representative for this, or any other population of hippopotami experiencing environmental stress. Assessment of impacts upon the riverine habitat provides more evidence of potential than actual deleterious effect.

Three primary possibilities exist that could precipitate a population crisis; 1) an increased, unchecked growth in the population under existing environmental conditions, 2) drought, an extended dry season, or the reversion of conditions to pre-1960 rainfall patterns (severe dry seasons), and 3) significant expansion of area devoted to agriculture, particularly crop production, within hippopotamus grazing range.

Population Status

A superabundance of forage resulting from increased dry season rainfall beginning in 1969 (Sinclair 1977), has sustained the hippopotamus population within the Mara River in an eruptive state. The population has expanded 25 fold since 1959, when the first estimate of the number of hippopotamus for the Mara River within Kenya was made (Darling 1960). Numbers within the 127 km census section will double, from 3000 to 6000, within six years if the observed rate of increase continues.

Density redistributions recorded between 1980 and 1982 were pronounced. This is interpreted as a density-dependent response to a combination of high occupancy rates and crowding within suitable pools within the Masai Mara National Reserve. Density of hippopotami within the Reserve remained near 25 per km of river between 1980 and 1982.

Average group size alone cannot be considered indicative of population size, as suggested by Laws and Parker (1968). Water fluctuations in the river affect group size on a daily basis. Group distribution, or the density of animals per unit length of river, are the only useful indicators of population size, and these are largely determined by the availability of suitable pools.

Table VII.1 presents recorded densities of hippopotami within rivers. Lake populations cannot be compared with riverine populations on a density/km basis as grazing is usually available only on one side of the lake. Most

Table VII.1. Recorded densities of hippopotami per Km of river.

Luangwa River, Zambia (Marshall and Sayer 1976)	
In North Lungwa Game Reserve	21.6/km
In South Luangwa Game Reserve	11.3/km
Kruger Park rivers, South Africa (Pienaar *et al.* 1966)	
Olifants River	2.4/km
Levubu River	1.3/km
Letaba River	3.1/km
Sabi River	4.1/km
Crocodile River	4.0/km
Outside Kruger Park, South Africa (Villijoen 1980)	
Olifants River	2.7/km
Blyde River	0.7/km
Mara River, Kenya (this study)	
1980	
In Masai Mara Game Reserve	24.1/km
Outside Masai Mara Game Reserve (55 km)	6.8/km
1982	
In Masai Mara Game Reserve	24.8/km
Outside Masai Mara Game Reserve (55 km)	19.8/km

literature enumerating hippopotamus populations provide data on animals/km of river or lakeshore, as presented in Table VII.1, but not on available grazing area. This must be estimated, and will be a conservative figure, as the effect of river meander to compress available grazing range is not taken into account. Table VII.2 presents estimated stocking rates taken from published literature and this study.

Population Limitations

Forage was available in abundance throughout the period of this study (Mar. 1981 - Nov. 1982). Ungulates were less numerous in the riverine than in the mid or upper catenas for all seasons, reducing potential competition between other herbivores and hippopotami for forage. Standing grass biomass increased with proximity to the river during both long and shortgrass seasons.

Hippopotamus trails extended further inland during the wet than the dry seasons. This was evidently due to a preference for the shortgrass grazing available in both the mid and upper catenas, where a variety of ungulates maintained shortgrass conditions over much of the range. Previous works indicate that hippopotami extend their grazing radius during the dry season, when forage is limited (Attwell 1963, Field 1970, Lock 1972).

There was no indication that the availability of forage exerted limiting pressures upon the growth of the hippopotamus population. Grassland within the study area is

Table VII.2 Available Grazing Area per Hippopotamus (based on an average forage Distance of 3.2 km. from each bank (Laws 1963)).

Queen Elizabeth National Park, Uganda (Lake Hippo Population)	
Total population (Bere 1959)	39.5 ha/hippopotamus
Mweya Peninsula (Laws 1963)	3.4 ha/hippopotamus
Kruger Park, South Africa (Pienaar *et al.* 1966)	
Olifants River	13.0 ha/hippopotamus
Levubu River	22.4 ha/hippopotamus
Lefaba River	98.7 ha/hippopotamus
Labi River	74.6 ha/hippopotamus
Crocodile River	77.3 ha/hippopotamus
Outside Kruger Park, South Africa (Villijoen 1980)	
Olifants River	102.6 ha/hippopotamus
Blyde River	614.5 ha/hippopotamus
Mara River, Kenya (this study)	
1980	
In Masai Mara Reserve	13.1 ha/hippopotamus
Outside Masai Mara Reserve	46.3 ha/hippopotamus
1982	
In Masai Mara Reserve	12.9 ha/hippopotamus
Outside Masai Mara Reserve	15.9 ha/hippopotamus

evidently maintained in a zootic-disclimax state by hippopotami, with a gradient towards a *Themeda* climax association increasing with distance from the river. Moderate grazing encourages increased grassland productivity (Pratt and Gwynne 1977, Sinclair and Norton-Griffiths 1979), and as there was evidence of only locally restricted areas of overgrazed range (around mineral licks and immediately adjacent to permanent pool locations), I contend that the grassland within my study area was not overgrazed during the period of this study. Thus, the moderate grazing pressure produced a zootic-disclimax sere along the river that provided optimal, or near-optimal conditions for hippopotami. This in turn may have provided sub-optimal conditions for animals dependent on long-grass for the bulk of forage requirements (J. Stelfox, Kenya Rangeland Eclolgical Monitoring Unit, pers. comm.). Animals such as elephant, cape buffalo and zebra are affected when long grass is scarce.

Social pressures within groups inhabiting the diurnal habitat did not reveal any mechanism that was acting to limit population growth during the study. Though aggression did tend to rise with the density of members within pools, related mortalities were few.

Laws and Clough (1966) indicated that fecundity may decrease in response to increased densities, though it was not determined whether decreases could have been caused by social stress or poor nutrition resulting from interspecific

competition for forage. Census results for the Mara River hipppopotami indicate that fecundity is not decreasing.

Density-depenent social pressure was the probable cause of the redistribution of hippopotamus densities into the northern half of the census section. If the population continues to expand, this redistribution will terminate with densities reflecting more closely the availablity of suitable diurnal habitat. The population expansion will then become locally focussed, and strong social pressures may limit population growth through stress-related reductions in fecundity, and increased mortality from fighting.

Environmental Impacts

Range conditions were not seriously affected by current hippopotamus utilization. The temporal distribution of rainfall that has resulted in high grassland productivity, has also allowed the grassland to resist hippopotamus induced succession.

The long term effects of nutrient loss to the river via hippopotamus feces is not known, though probable effects are reduced topsoil genesis and lowered soil fertility. Range fires may be excluded from areas used by hippopotami for grazing, resulting in an expansion of the riverine forest.

Bank degradation was an ongoing process strongly linked to hippopotamus densities within the river. Both the use of mineral digs and paths cut into the bank result in the movement of soil into the river, and alterations in channel

configuration. As hippopotami appear to avoid pool areas with soft silty bottoms, the deposition of soil removed from the banks may cause a reduction of suitable pools within the river. Sheet erosion was not common, indicating that soil compaction and/or over-utilization of range immediate to the river was not causing substantial topsoil erosion.

Human-hippopotamus conflict was evident along the northern extent of the census section. The existence of farming operations, particularly small vegetable plots, has resulted in some control shooting of hippopotami. Provided the rainfall regime in the area maintains crop production, such conflicts will continue. The subdivision of group ranches along the Mara River, proposed by the Kenya government in 1983, will provide more individual control of rangeland by Masai and further incentive for agricultural activities.

The present range of hippopotami throughout Africa is a fraction of former distribution. The primary causes of population reductions have been hunting (for ivory and meat) and conflict with agriculture (Kingdon 1979). Kingdon (*op. cit.*) presents a map of hippopotamus distribution throughout East Africa. Recently eliminated populations are included and these mainly coincide with areas of agricultural expansion.

The expanding hippopotamus population north of the Masai Mara National Reserve was met by increased human settlement in the area during the 1980 - 1982 period. If the

Hippopotamus population of the Mara River continues to expand, a management plan will have to be formulated.

LITERATURE CITED

Andere, D.K. (ed.) 1980. Kenya Rangeland Ecology Monitoring Unit Annual Report 1978-1979. Kenya Ministry of Wildlife and Tourism.

Ansell, W.F.H. 1965. Hippo census on the Luangwa River. *Puku* 3: 15-27.

Ansell, W.F.H. 1965A. Feeding habits of *Hippopotamus amphibius* (Linn.). *Puku* 3: 171.

Attwell, R.I.G. 1963. Surveying Luangwa hippo. *Puku* 1: 29-50.

Bere, R.M. 1959. Queen Elizabeth National Park, Uganda. The hippopotamus problem and experiment. *Oryx* 5: 116-124.

Darling, F.F. 1960. An ecological reconnaissance of the Mara Plains in Kenya Colony. *Wildl. Monogr.* 5.

DeVos, A. and H.S. Mosby. 1971. Habitat analysis and evaluation. In: Wildlife Management Techniques. pp. 135-174. The Wildlife Society. Washington.

Dittrich, L. 1976. Age of sexual maturity in the hippopotamus *Hippopotamus amphibius*. *Int. Zoo Yearbook* 16: 171-173.

Dodds, D.G. and D.R. Patton, 1968. Report to the Government of Zambia on wildlife and land use survey of the Luangwa valley. U.N. Development programme F.A.O. no. TA 2591. Rome.

Eltringham, S.K. 1974. Changes in the large mammal community of Kweya peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. *J. Appl. Ecol.* 11:

855-866.

Epp, H. and J. Agatsiva 1980. Habitat types of the Mara-Narok area, western Kenya. *KREMU tech. rep.* series no. 20.

Field, C.R. 1970. A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius*) in the Queen Elizabeth Park, Uganda, with some management implications. *Zool. Africana* 5: 71-86.

Giest, V. 1966. The evolution of horn-like organs. *Behaviour* 20: 377-416.

Grzimek, B. 1972. Grzimek's Animal Life Encyclopedia. Ch. 5. Vol.13. Van Nostrand Reinhold Press. Munich.

Hediger, H. 1951. Observations sur la psychologie animale dans les Parcs Nationaux du Congo Belge. Inst. Parcs Nationaux du Congo Belge, Bruxelles.

Herring, S.W. 1975. Adaptations for gape in the hippopotamus and its relatives. *Forma Functio.* 8: 85-100.

Karstad, E.L., Hudson, R.J., Stelfox, J.G. and S. Mbugua 1980. Census of hippopotamus populations in the Mara River system, 1980. *KREMU tech. rep.* series No. 18.

Kingdon, J. 1979. East African mammals; an atlas of evolution in Africa. *Vol. III part B* Academic Press. London.

Klingel, H. 1979. Social organisation of *Hippopotamus amphibius*. (abstract) *Verh. Dtsch. Zool. Ges.* 1979: 241.

Kuchar, P. 1979. A methodology for sampling vegetation. *KREMU tech. rep.* series No. 16.

Laws, R.M. 1963. Report and accounts of the Uganda National Parks. *Uganda Argus*, Kampala.

Laws, R.M. 1968. Dentition and ageing of the hippopotamus. *E. Afr. Wildl. J.* **6**: 19-52.

Laws, R.M. and G. Clough. 1966. Observations on reproduction in the hippopotamus, *Hippopotamus amphibius*. *Symp. Zool. Soc. Lond.* No. **15**: 117-140.

Laws, R.M. and I.S.C. Parker 1968. Recent studies on elephant populations in East Africa. *Symp. Zool. Soc. Lond.* **21**: 319.

Leuthold, W. 1977. African ungulates: a comparative review of their ethology and behavioural ecology. Springer-Verlag. Bonn.

Lock, J.M. 1972. The effects of hippopotamus grazing on grasslands. *J. Ecol.* **60**: 445-467.

Mackie, C. 1976. Feeding habits of the hippopotamus on the Lundi River, Rhodesia. *Arnoldia* (Rhod.) **7**: 1-16.

Marshall, P.J. and J.A. Sayer. 1976. Population ecology and response to cropping of a hippopotamus population in eastern Zambia. *J. Appl. Ecol.* **13**: 391-404.

Mwenge International Associates Ltd., 1980. *A Study on the Management of Very Large Herbivores in Kenya.* Final report to the Ministry of Environment and Natural Resources, Kenya. 1008 pp.

Neu, C.W., Byers, C.R., and J.M. Peek 1974. A technique for the analysis of utilization-availability data. *J. Wildl. Manage.* **38**: 541-545.

Olivier, R.C.D. and W.A. Laurie. 1974. Habitat utilization by hippopotamus in the Mara River. *E. Afr. Wildl. J.* **12**: 249-271.

Owen-Smith, N. 1977. On territoriality in Ungulates and an evolutionary model. *Quart. Rev. Biol.* **52**: 1-38.

Pienaar, U. De V., Van Wyk, P. and N. Fairall. 1966. An experimental cropping scheme of hippopotamus in the Letaba River of the Kruger National Park. *Koedoe* **9**: 1-33.

Plowright, W., Laws, R.M. and Rampton, C.S. 1964. Serological evidence for the susceptibility of the hippopotamus (*Hippopotamus amphibius* Linnaeus) to natural infection with rinderpest virus. *J. Hyg.* **62**: 239-36

Pratt, D.J. and M.D. Gwynne. 1977. Rangeland Management and Ecology in East Africa. Hodder and Stoughton. London.

Scotcher, J.S.B., Stewart, D.R.M. and C.M. Breen, 1978. The diet of hippopotamus in Ndumu Game Reserve, Natal, as determined by faecal analysis. *Afr. J. Wildl. Res.* **8**: 1-11.

Sinclair, A.R.E. 1977. The African Buffalo. The University of Chicago Press. Chicago.

Sinclair, A.R.E. and M. Norton-Griffiths 1979. Serengeti; Dynamics of an Ecosystem. The University of Chicago Press. Chicago.

Skinner, D.J., Scorer, J.A. and Millar, R.P. 1975. Observatiopns on the reproductive physiological status

of mature herd bulls, and young bulls in the hippopotamus *Hippopotamus amphibius* Linnaeus. *Gen. Comp. Endocrin.* **26**: 92-95.

Smuts, G.L. and I.J. Whyte. 1981. Relationships between reproduction and environment in the hippopotamus *Hippopotamus amphibius* in the Kruger National Park. *Koedoe* **24**: 169-185.

Spinage, C.A. 1958. Hippos galore. The Kazinga Channel and its hippo problem. *Afr. Wildl.* **13**: 117-121.

Stelfox, J.G., Kufwafwa, J.W., Mbugua, S.W. and D.G. Peden. 1979. Livestock and wild herbivore populations in the Kenya rangelands in 1977 compared with 1978. *KREMU tech. rep.* series no. 6.

Stelfox, J.G., Peden, D.G., Mbugua, S.W. and R.J. Hudson. 1980. Populations, stocking rates & distributions of wildlife & livestock on Mara & Loita Plains: December 1978-November 1979. *KREMU tech. rep.* series no. 19.

Thornton, D.D. 1971. The effect of complete removal of hippopotamus on grassland in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.* **9**: 47-55.

Verheyen, R. 1954. Monographie ethologique de l'hippopotame (*Hippopotamus amphibius* Linn.). *In* Explor. Parc Natl. Albert *Inst. Parcs Nat. Congo Belge, Brussels.*

Vesey-Fitzgerald, D.F. 1960. Grazing succession among East African game animals. *J. Mammal.* **41** (2): 161-172.

Villijoen P.C. 1980. Distribution and numbers of the hippopotamus in the Olifants and Blyde rivers. *S. Afr.*

Wildl. Res. **10**: 129-132.

Yoaciel, S.M. 1981. Changes in the populations of large herbivores and in the vegetation community in Mweya Peninsula, Rwenzori National Park, Uganda. *Afr. J. Ecol.* **19**: 303-312.

Young, E. 1966. Nutrition of the hippopotamus *Hippopotamus amphibius*. *Afr. Wildl.* **20**: 165-167.

APPENDICES

APPENDIX 1

River Current and Width Measurements

River current and width measurements were taken over a 10 km stretch of river, as part of an investigation into habitat selection by hippopotami. The tabled data present records taken on four different days. Measurement points were 500 m apart and staggered between sessions, resulting in 80 measurement points in total at 125 m intervals. River current and widths are in part related to the particular water levels (recorded at the field camp) for each session. The number of hippopotami within each 50 m measurement length (bounded by up and downstream widths) were recorded.

Session #1 17/11/81, water level= 0.70 m.

Speed m/sec	upstrm width(m)	dwnstr width(m)	# hippo, if present
1.22	29	28	14
1.45	30	31	
1.39	32	30	55
1.01	25	28	
0.56	26	23	
1.12	22	25	
0.44	23	22	
0.55	28	28	
0.56	27	33	
0.52	23	26	
1.38	28	36	4
0.55	24	28	
1.18	29	35	1
1.54	41	48	3
1.58	36	37	3
1.17	41	43	2
2.26	34	32	7
0.55	31	26	
1.13	35	32	
1.31	31	33	6

Session #2 09/01/82, water level= 0.48 m.

Speed m/sec	upstrm width(m)	dwnstr width(m)	# hippo, if present
0.33	21	27	
0.56	21	23	9
0.16	30	32	
0.31	33	32	
0.67	17	14	
0.47	21	24	
0.79	23	25	
0.68	21	24	
0.69	29	31	
0.50	19	30	
0.16	25	27	6
0.54	26	31	
0.31	30	27	
0.18	31	30	
0.18	35	39	120
0.15	29	36	1
0.15	29	35	
0.62	23	28	
0.18	31	19	5
0.25	30	28	

Session #3 07/05/82, water level= 0.88 m.

Speed m/sec	upstrm width(m)	dwnstr width(m)	# hippo, if present
0.78	37	33	
0.41	29	30	2
0.81	36	30	
0.79	23	24	
0.93	22	18	
0.82	31	28	
0.77	29	29	
1.16	25	24	
0.53	33	29	2
0.51	30	30	6
0.47	26	28	2
1.32	15	26	
0.54	31	28	
0.64	32	33	1
0.77	31	30	5
0.41	34	31	
0.57	31	30	
1.02	26	29	1
0.55	33	29	12
0.44	38	35	3

Session #4 06/06/82, water level= 1.31 m.

Speed m/sec	upstrm width(m)	dwnstr width(m)	# hippo, if present
1.03	31	32	
1.02	29	32	
1.38	42	45	
1.27	25	30	4
1.95	27	24	
1.69	35	31	
1.40	35	38	
2.24	30	34	
2.46	31	33	
1.32	35	36	15
1.82	25	23	
1.92	31	27	10
1.14	37	30	
0.87	35	37	41
1.14	41	35	
1.91	35	36	1
1.15	34	29	1
1.18	37	32	
1.04	33	26	

APPENDIX 2

Recorded Mortalities and the Ages of Collected Skulls

Hippopotamus mortalities were recorded from Mar. 1981 to Nov. 1982. Most observations were made within the 10 km of river adjacent to the field camp, though reported deaths were investigated over a large area.

Thirteen skulls were collected from both within and outside the Masai Mara National Reserve. Skulls were aged according to Laws' (1968) toothwear criteria.

Old skulls, without remnants of the carcass, were sexed tentatively by examination of the bone structure. Sexual dichotomy is evident in bone structure at points of muscle insertion. Males exhibit markedly more massive occipital processes, zygomatic arches, and saggital crests than do females.

Carcasses simply spotted in the river and not recovered (crocodiles were usually in attendance) could not always be sexed. A rough age class was assigned based upon body size.

Recorded Mortalities

Sixteen mortalities were recorded from within a 10 km section of river containing on-average, 215 hippopotami, from March 1981 to October 1982 (Table A2.1).

Table A2.1. Reported and observed mortalities of hippopotami within the Mara River.

Mort. Date	Obsvtn/ Report	Cause	No. Hippo	Skull No.	Age Class	Sex
03/81	R	flood	3		young	*
07/81	R	lion	1	8	9-11 yrs	m
08/81	O	fight	1	7	19-25 yrs	?f
02/82	R	*	1		Adult	*
02/82	O	*	1	3	8-12 yrs	f
04/82	O	crocodile	1	2	2-10 days	m
04/82	O	*	1		2-10 days	*
05/82	O	*	1		Adult	f
05/82	O	*	1		Adult	m
05/82	O	*	1		Adult	f
06/82	O	*	1		Adult	f
06/82	O	*	1		Calf	*
06/82	O	rabies?	1		SubAdult	m
06/82	O	*	1		Adult	*
07/82	O	fight	1	1	6.5-10.5 yrs	m
07/82	O	*	1		Adult	*
07/82	O	*	1		SubAdult	m
07/82	O	*	1		Calf	*
10/82	O	*	1		Adult	m
10/82	O	*	1		Adult	f
10/82	O	fight	2		Adults	m/m
03/83	R	flood	5+		Young	*

The relatively high number of mortalities attributable to flood drowning are of intrest. According to reports, all drowned animals were young. It would appear that flood related drownings are density-independent occurances, and that weight and/or learned behaviour may play a role in resisting or avoiding dangerous flood conditions. The confluences of seasonal drainage channels with the river are often used by groups as refuges from the swift currents and debris in the flood swollen river.

Estimated Ages of Collected Skulls

Table A2.2 presents the estimated ages of the 13 skulls collected during the field program. In presenting the ageing criteria, Laws (1968) notes that the rates of tooth wear may vary from place to place dependent on the amount of abrasives, such as silica and soil, in the diet.

The ageing criteria must be used with some circumspection, only 6 known-age jaws were avalable to Laws (*op. cit.*), none of which were under 15 years of age. The latter is of particular importance as much of the younger year estimates are based upon tooth eruption, a process nearly completed by 15 years of age.

The average estmated age of skulls collected along the Mara River was 17.7 ± 2.5 years. If this is to be compared with the 'initial expectation of life' presented by Laws (1968), the sample average age estimate appears high. The initial expectation of life generated from Laws' (*op. cit.*) Kazinga Channel population survivorship curves is 10.1 and 9.3 for the two models presented. As only one skull younger than the subadult class was collected during this study, it can be assumed that younger age classes are underepresented. Scavengers on land, particularly hyena, could crush the small, softer jaws of young hippopotami. In addition, all young animals recorded dead (5 calves and neonates) were spotted in the river, with only one skull recovered. All skulls found on land were collected.

Table A2.2 Estimated ages of collected skulls (from tooth wear criteria by Laws, 1968).

Skull No.	Est. Age	Sex
1	6.5-10.5 yrs	m?
2	2-10 days	m
3	8.0-12.0 yrs	f
4	25.0-31.0 yrs	m?
5	19.0-25.0 yrs	?
6	30.0-36.0 yrs	m
7	19.0-25.0 yrs	m
8	9.0-13.0 yrs	f?
9	14.5-20.5 yrs	f
10	19.5-25.5 yrs	m
11	20.5-26.5 yrs	?
12	15.0-21.0 yrs	f?
13	11.5-15.5 yrs	?

APPENDIX 3

Estimating Herbage Biomass by the Horizontal Intercept Method.

The horizontal intercept method was designed for this study in response to a need for easily transported (on foot) equipment used to accurately record data. As the only goal of the technique was to record data for estimating standing grass biomass, a frame and wire technique, as developed by McNaughton (Sinclair and Norton-Griffiths 1979) used to record of individual specie biomass, was not necessary.

The ocular estimation method used by KREMU (Kuchar 1979) in the Mara area, is appropriate for large sample sizes. For this project the applicability was low, as relatively few estimates were made and the subjectivity of the method would have introduced a large error.

Measurements involve both plant basal cover and the density of vegetative parts at specific heights in the sward. Basal cover is determined by recording the hits on grass bases every 2 cm along a marked 1 m long metal rod. Height and density (cross-sectional structure) are determined by counting the number of hits for all vegetative parts (stems, leaves etc.) at 10, 30, 50 and 80 cm above ground.

The rod is held in a horizontal position for the latter counts by fitting one end of the rod in holes drilled at the appropriate heights in a spike-ended staff driven firmly into the ground.

Calibration

One hundred 1 m^2 clip plots were collected and samples air dried to calibrate the technique. Clip-plots used for calibration were collected over 14 months, and were distributed evenly along 10 km of river adjacent to the field camp. All plots were located within 50 m of the river, and an effort was made to collect samples representative of the area's average standing grass biomass. Forbs, though not commonly appearing in samples, were included.

Stepwise multiple regression analysis of horizontal intercept data and dry weights from 100 1 m^2 clips produced an R^2 value of 0.70 for the third dependent variable entered. The first (and strongest) predictor was the 10 cm level horizontal intercept (R^2=0.65). The second value entered into the equation was the 30 cm horizontal intercept, raising the R^2 value to 0.68. Basal cover was the third variable. Measurement levels of 50 and 80 cm were not included in the predictor equation, as adjusted R^2 values decreased subsequent to the inclusion of the third dependent variable. The equation generated was;

Biomass (dry)= -3.307 + (GND x 8.16) + (CM10 x 3.05) + (CM30 x 3.73)

Residual variance is probably due to three main factors; 1) clipping error, 2) counting error, particularly in thick long-grass plots where some movement of grasses is necessary in order to view the rod, and 3) air drying. The latter may have been a major source of error, particularly during wet periods when air humidity determines the minimum moisture content in dried samples. Daily relative humidity records were not kept.

The large sample size of calibration clip samples was reflected in the calculated P value of the third (and final) step in the multiple regression analysis. The technique provided 70% precision greater than 99% of the time ($P < 0.001$). The calibration of this technique for other grasslands would likely require substantially fewer clip plots to provide similar precision at the 10% confidence level.

An important feature of this technique is the inclusion of a basal cover measurement. Compensatory growth of grasses under sustained grazing pressure by hippopotamy has been documented by Field (1970), Thornton (1971) and Olivier and Laurie (1974), and involves increases in mat-forming species. This increases vegetative biomass within the first few centemeters above ground.

Basal cover data were included into the step-wise multiple regression analysis as the third variable entered, and had a strong positive association with predicted dry weight biomass. This included the biomass of very low-lying

species into the estimate, an important aspect of sampling grazing mosaics.

Overall, the horizontal intercept method proved to be a quick and relatively accurate method of measuring standing grass biomass. The necessary equipment is simple, a graduated spike-tipped staff and a wire rod marked a 2 cm intervals. Each complete measurement session takes approximately 2 minutes, and accuracy (repeatability) is high, as very little subjectivity is involved in the sampling process.

Clip Plot Records

Clip plot samples were obtained from 1 m^2 plots located on a stratified random basis along the Mara River. Prior to clipping at ground level, grasses within plots were measured according to the horizontal intercept method described. Grasses were placed in cloth bags and air dried for not less than 48 hours. Both wet and dry weight data are presented.

Forage availability was sampled in this manner from 19/09/81 through to 04/10/82, providing information on the standing grass biomass and phenology over more than one complete seasonal cycle.

Dates, recorded 'hits' at the respective levels by the horizontal intercept method, and wet and dry weights are tabled. With the exception of the first 8 sampling days, three plots were measured and clipped per session.

Clipplot data

Date	Ground	10cm	30cm	50cm	Wet wt. !	Dry wt. !
19/09/81	12	34	32	17	nc	513
19/09/81	15	07	04	02	nc	123
03/10/81	16	31	10	03	nc	235
03/10/81	16	31	08	03	nc	147
06/10/81	12	01	00	00	nc	19
06/10/81	10	41	21	05	nc	249
07/10/81	13	36	14	06	421	346
07/10/81	07	13	01	00	202	127
10/10/81	18	68	11	04	695	455
10/10/81	12	42	06	00	437	286
13/10/81	12	73	03	01	470	300
13/10/81	10	92	18	09	nc	795
22/10/81	16	94	30	11	nc	560
22/10/81	15	78	02	00	663	500
01/11/81	10	97	52	03	500	435
01/11/81	08	31	03	02	335	295
15/11/81	10	56	07	00	530	415
15/11/81	09	27	02	01	365	293
15/11/81	14	28	00	00	240	208
09/12/81	09	20	03	00	265	190
09/12/81	07	13	02	00	223	180
09/12/81	09	59	10	01	470	345
11/12/81	08	87	23	06	785	560
11/12/81	13	52	12	06	670	500
11/12/81	11	33	02	00	475	300
16/12/81	10	33	04	01	320	240
16/12/81	09	02	02	01	405	312
13/12/81	13	66	10	04	815	545

! (g/m^2)

Date	Ground	10cm	30cm	50cm	Wet wt.	Dry wt.
08/01/82	11	06	00	00	52	45(g)
08/01/82	09	100	06	00	738	465
08/01/82	09	48	01	00	429	255
24/02/82	04	04	00	00	110	82
24/02/82	11	09	00	00	122	91
24/02/82	08	26	02	00	310	187
07/03/82	12	01	00	00	57	47
07/03/82	08	29	02	00	187	134
07/03/82	13	03	00	00	103	81
19/03/82	10	00	00	00	nc	80*
19/03/82	09	03	00	00	nc	80*
19/03/82	09	02	00	00	122	106
23/03/82	10	49	07	00	438	300
23/03/82	12	30	00	00	220	160
23/03/82	09	00	00	00	nc	70*
09/04/82	09	09	01	00	155	77
09/04/82	05	04	00	00	147	80
09/04/82	05	06	00	00	120	65
01/05/82	12	03	00	00	119	52
01/05/82	12	51	01	00	575	345
01/05/82	15	19	02	00	190	80
08/05/82	09	31	02	00	372	190
08/05/82	10	07	04	01	152	88
08/05/82	07	08	01	01	145	68
30/05/82	11	44	03	01	250	140
30/05/82	16	107	46	16	1070	725
30/05/82	09	09	02	00	95	45
02/06/82	13	03	00	00	57	35
02/06/82	08	12	02	01	155	62
02/06/82	09	33	06	06	320	147

Date	Ground	10cm	30cm	50cm	Wet wt.	Dry wt.
07/06/82	09	38	14	09	340	180(g)
07/06/82	08	126	28	22	735	490
07/06/82	08	05	03	00	105	67
20/06/82	08	07	00	01	37	33
20/06/82	08	58	22	08	625	345
20/06/82	11	57	07	00	340	195
27/06/82	09	86	24	18	680	330
27/06/82	07	47	15	05	355	177
27/06/82	04	00	00	00	nc	30*
11/07/82	09	79	12	02	487	250
11/07/82	10	146	27	07	980	550
11/07/82	13	06	03	02	85	40
19/07/82	05	03	00	00	40	38
19/07/82	06	41	05	00	175	142
19/07/82	07	65	04	01	199	150
26/07/82	05	02	00	01	137	115
26/07/82	07	24	06	02	290	225
26/07/82	09	75	10	00	547	387
13/08/82	13	48	28	10	503	320
13/08/82	15	34	08	00	388	225
13/08/82	14	07	01	00	94	65
28/08/82	13	18	04	00	182	115
28/08/82	13	05	01	00	76	62
28/08/82	12	01	00	00	nc	90*
01/09/82	06	48	01	00	355	265
01/09/82	07	20	00	00	251	240
01/09/82	08	02	00	00	nc	70*
06/09/82	14	24	10	04	255	175
06/09/82	09	04	01	04	65	51
06/09/82	12	00	00	00	nc	94

Date	Ground	10cm	30cm	50cm	Wet wt.	Dry wt.
09/09/82	06	05	02	00	78	58(g)
09/09/82	11	00	00	00	nc	86*
09/09/82	06	00	00	00	nc	45*
28/09/82	07	21	00	00	220	142
28/09/82	09	12	00	00	130	85
28/09/82	09	00	00	00	nc	70*
01/10/82	11	39	01	00	395	255
01/10/82	12	13	00	00	142	100
01/10/82	12	00	00	00	nc	90
04/10/82	09	05	00	00	35	24
04/10/82	09	00	00	00	nc	70*
04/10/82	08	00	00	00	nc	60*

* Weights estimated, grass too short to collect.

APPENDIX 4

Ungulate Census, Sept./81 - Oct./82.

The following data were recorded from weekly (with some gaps) ground counts of ungulates over a 32 km fixed circuit. Observations were made from a vehicle, and all ungulates within 200 m of either side of the vehicle were identified to species, number observed, and location within the riverside catena covered (low, medium and high).

The counts covered the period from 16/09/81 to 09/10/82 and were conducted in order to determine the intensity and distribution of grazing pressures exerted by ungulates within the grazing range of the hippopotamus population within the Mara River. Of special interest is the temporal distribution of wildebeest, zebra, and Thomson gazelle; the major migratory species.

1: Wildebeest

Date	*Catena:*	Low	Med.	High	Total
16/09/81		8	329	8	345
20/09/81		0	112	141	284
04/10/81		0	667	413	1080
11/10/81		67	2132	70	2269
27/10/81		103	571	440	1114
13/11/81		38	223	164	425
08/12/81		584	937	71	1592
13/12/81		706	1267	164	2137
20/12/81		257	716	19	992
07/01/82		1	111	4	116
12/01/82		0	57	12	69
20/01/82		2	35	6	43
01/02/82		0	66	61	127
07/02/82		0	192	22	114
14/02/82		0	125	6	131
22/02/82		4	103	1	108
01/03/82		22	461	0	483
08/03/82		245	300	26	571
18/03/82		257	1664	146	2067
24/03/82		63	1305	68	1436
30/03/82		40	1123	101	1264
07/04/82		0	2086	79	2165
13/04/82		443	1296	10	1749
27/04/82		0	53	52	105
04/05/82		0	36	1	37
10/05/82		0	12	2	14
29/05/82		0	21	0	21
05/06/82		0	13	0	13
10/06/82		0	24	2	26
19/06/82		0	5	12	17
27/06/82		0	74	39	113
09/07/82		0	327	199	526
15/07/82		0	510	819	1329
23/07/82		0	272	422	694
29/07/82		6	298	166	470
13/08/82		82	3698	688	4468
27/08/82		51	1349	1818	3218
02/09/82		56	136	35	277
12/09/82		64	2298	75	2437
25/09/82		198	657	0	855
03/10/82		425	1757	252	2434
09/10/82		306	992	109	1407

2: Zebra

Date	*Catena:*	Low	Med.	High	Total
16/09/81		88	100	0	188
20/09/81		94	189	1	284
04/10/81		0	227	0	227
11/10/81		189	130	0	319
27/10/81		170	153	0	323
13/11/81		254	79	9	342
08/12/81		915	206	0	1121
13/12/81		314	378	6	698
20/12/81		307	217	28	552
07/01/82		26	32	44	102
12/01/82		21	28	0	49
20/01/82		6	37	57	100
01/02/82		0	28	124	152
07/02/82		16	322	26	364
14/02/82		8	142	0	150
22/02/82		12	356	0	368
01/03/82		20	205	15	240
08/03/82		71	169	6	246
18/03/82		139	66	14	219
24/03/82		58	133	4	195
30/03/82		0	8	0	8
07/04/82		0	68	0	68
13/04/82		2	4	0	6
27/04/82		11	215	48	274
04/05/82		0	66	66	122
10/05/82		0	24	34	58
29/05/82		0	14	46	60
05/06/82		0	30	27	57
10/06/82		0	89	17	106
19/06/82		0	276	179	455
27/06/82		5	30	15	50
09/07/82		5	124	37	166
15/07/82		0	251	5	256
23/07/82		0	32	9	41
29/07/82		49	138	23	270
13/08/82		0	4	0	4
27/08/82		3	16	0	19
02/09/82		4	27	0	31
12/09/82		94	135	0	229
25/09/82		26	52	52	130
03/10/82		21	65	2	88
09/10/82		80	140	72	292

3: Topi

Date	*Catena:*	Low	Med.	High	Total
16/09/81		8	21	2	31
20/09/81		15	45	1	88
04/10/81		9	84	16	109
11/10/81		8	30	7	45
27/10/81		6	25	5	36
13/11/81		17	7	25	49
08/12/81		35	56	11	102
13/12/81		52	51	9	112
20/12/82		83	39	16	138
07/01/82		23	64	22	109
12/01/82		0	83	22	105
20/01/82		36	76	64	176
01/02/82		21	88	74	183
07/02/82		0	85	55	140
14/02/82		12	122	39	173
22/02/82		0	163	10	173
01/03/82		13	99	4	116
08/03/82		51	65	10	126
18/03/82		29	18	3	50
24/03/82		1	20	6	27
30/03/82		26	17	6	49
07/04/82		1	52	16	69
13/04/82		66	46	6	118
27/04/82		17	56	14	87
04/05/82		13	62	57	132
10/05/82		0	108	79	187
29/05/82		0	14	32	46
05/06/82		0	27	61	88
10/06/82		0	105	135	240
19/06/82		0	61	112	173
27/06/82		12	92	135	239
09/07/82		13	125	78	216
15/07/82		0	84	26	110
23/07/82		0	48	28	76
29/07/82		0	28	14	42
13/08/82		0	51	9	60
27/08/82		0	54	19	73
02/09/82		1	22	40	63
12/09/82		33	49	7	89
25/09/82		39	46	20	105
03/10/82		21	44	35	100
09/10/82		48	16	13	77

4: Thomson Gazelle

Date	*Catena:*	Low	Med.	High	Total
16/09/81		23	115	50	188
20/09/81		84	188	110	382
04/10/81		0	256	189	445
11/10/81		10	121	149	280
27/10/81		1	252	131	384
13/11/81		27	174	131	332
08/12/81		26	287	50	363
13/12/81		83	243	89	415
20/12/82		15	232	101	348
07/01/82		18	177	125	320
12/01/82		13	162	132	307
20/01/82		41	254	393	488
01/02/82		4	272	341	617
08/02/82		0	197	239	346
14/02/82		0	213	262	275
22/02/82		0	195	87	282
01/03/82		6	312	78	396
08/03/82		10	278	186	474
18/03/82		12	122	55	199
24/03/82		2	299	263	564
30/03/82		0	162	113	275
07/04/82		0	328	198	526
13/04/82		7	368	63	428
27/04/82		0	79	26	105
04/05/82		0	69	270	339
10/05/82		0	51	383	434
29/05/82		0	130	198	328
05/06/82		0	157	411	568
10/06/82		1	101	247	348
19/06/82		0	276	501	777
27/06/82		0	420	350	770
09/07/82		2	420	360	782
15/07/82		1	560	288	848
23/07/82		0	291	467	758
29/07/82		37	197	319	563
13/08/82		62	221	86	369
27/08/82		48	238	72	358
02/09/82		33	270	167	470
12/09/82		28	262	143	433
25/09/82		47	280	221	548
03/10/82		0	442	426	868
09/10/82		37	257	273	567

5: Grant's Gazelle

Date	*Catena:*	Low	Med.	High	Total
16/09/81		3	1	0	4
20/09/81		0	0	2	2
04/10/81		0	8	5	13
11/10/81		0	6	3	9
27/10/81		0	6	0	6
13/11/81		0	0	5	5
08/12/81		0	20	3	23
13/12/81		2	28	9	39
20/12/82		9	12	2	23
07/01/82		0	8	13	21
12/01/82		5	12	5	22
20/01/82		0	3	1	4
01/02/82		8	17	2	27
07/02/82		0	9	4	13
14/02/82		0	5	5	10
22/02/82		0	16	5	21
01/03/82		0	9	2	11
08/03/82		4	7	0	11
18/03/82		0	0	0	0
24/03/82		2	7	0	9
30/03/82		3	14	3	20
07/04/82		0	22	1	23
13/04/82		0	25	0	25
27/04/82		0	1	1	2
04/05/82		0	6	4	10
10/05/82		0	8	18	26
29/05/82		0	21	23	44
05/06/82		0	18	15	33
10/06/82		0	25	13	38
19/06/82		0	6	36	42
27/06/82		0	11	18	29
09/07/82		0	0	25	25
15/07/82		2	21	2	25
23/07/82		0	5	12	17
29/07/82		4	5	5	14
13/08/82		0	4	2	6
27/08/82		0	3	3	6
02/09/82		0	0	17	17
12/09/82		0	17	7	24
25/09/82		8	5	3	16
03/10/82		0	9	5	14
09/10/82		0	39	12	51

6: Cape Buffalo

Date	*Catena:*	Low	Med.	High	Total
06/19/81		0	0	0	0
20/09/81		2	57	0	59
04/10/81		0	4	2	8
11/10/81		0	4	0	4
27/10/81		0	3	0	3
13/11/81		0	6	0	6
08/12/81		0	6	0	6
13/12/81		10	12	0	22
20/12/82		0	3	0	3
07/01/82		0	4	10	14
12/01/82		6	27	0	33
20/01/82		0	14	0	14
01/02/82		17	8	0	25
07/02/82		0	5	0	5
14/02/82		0	42	1	43
22/02/82		2	72	3	77
01/03/82		5	24	0	29
08/03/82		3	0	0	3
18/03/82		2	2	0	4
24/03/82		2	0	0	2
30/03/82		4	0	0	4
07/04/82		0	0	0	0
13/04/82		6	2	0	8
27/04/82		2	4	0	6
04/05/82		26	5	3	34
10/05/82		0	75	0	75
29/05/82		9	3	0	12
05/06/82		12	0	0	12
10/06/82		4	2	0	6
19/06/82		0	54	12	68
27/06/82		0	0	0	0
09/07/82		0	0	0	0
15/07/82		0	0	0	0
23/07/82		0	0	0	0
29/07/82		0	0	0	0
13/08/82		0	0	1	1
27/08/82		0	0	0	0
02/09/82		0	0	0	0
12/09/82		0	57	0	57
25/09/82		0	3	4	7
03/10/82		2	0	2	4
09/10/82		5	18	25	48

7: Waterbuck

Date	*Catena:*	Low	Med.	High	Total
16/09/81		2	0	0	2
20/09/81		0	0	0	0
04/10/81		0	28	0	28
11/10/81		0	0	0	0
27/10/81		2	0	0	2
13/11/81		0	0	0	0
08/12/81		7	0	0	7
13/12/81		0	0	0	0
20/12/82		13	0	0	13
07/01/82		0	0	0	0
12/01/82		0	0	0	0
20/01/82		14	12	0	26
01/02/82		0	0	0	0
07/02/82		0	0	0	0
14/02/82		0	1	0	1
22/02/82		2	1	0	3
01/03/82		0	0	0	0
08/03/82		0	0	0	0
18/03/82		0	0	0	0
24/03/82		0	0	0	0
30/03/82		0	0	0	0
07/04/82		0	0	0	0
13/04/82		0	0	0	0
27/04/82		0	0	1	1
04/05/82		0	0	0	0
10/05/82		0	0	0	0
29/05/82		0	0	1	1
05/06/82		0	0	0	0
10/06/82		0	0	3	3
19/06/82		0	3	0	3
27/06/82		0	0	0	0
09/07/82		0	0	0	0
15/07/82		0	0	0	0
23/07/82		0	0	0	0
29/07/82		0	0	0	0
13/08/82		0	0	0	0
27/08/82		0	0	0	0
02/09/82		0	0	0	0
12/09/82		0	0	0	0
05/09/82		0	0	0	0
03/10/82		0	0	0	0
09/10/82		0	0	0	0

8: Impala

Date	*Catena:*	Low	Med.	High	Total
16/09/81		3	18	17	38
20/09/81		31	39	0	70
04/10/81		1	176	2	179
11/10/81		2	6	6	14
27/10/81		0	9	3	12
13/11/81		0	0	5	5
08/12/81		97	101	0	198
13/12/81		13	96	0	112
20/12/82		83	44	26	153
07/01/82		18	6	1	25
12/01/82		13	15	1	29
20/01/82		79	186	4	269
01/02/82		4	151	0	155
07/02/82		0	119	5	124
14/02/82		18	147	1	166
22/02/82		2	26	0	28
01/03/82		4	3	0	7
08/03/82		2	100	1	103
18/03/82		27	1	0	28
24/03/82		6	4	12	22
30/03/82		4	22	0	26
07/04/82		3	15	0	18
13/04/82		3	2	0	5
27/04/82		6	36	0	42
04/05/82		78	7	3	88
10/05/82		0	68	3	71
29/05/82		1	79	2	82
05/06/82		39	10	170	219
10/06/82		0	73	31	104
19/06/82		0	9	25	34
27/06/82		4	9	31	44
09/07/82		0	0	26	26
15/07/82		0	76	1	77
23/07/82		37	9	12	58
29/07/82		4	44	0	48
13/08/82		10	1	2	13
27/08/82		8	13	0	21
02/09/82		0	21	0	21
12/09/82		38	4	63	105
25/09/82		4	76	0	80
03/10/82		0	103	8	111
09/10/82		21	4	8	33

9: Warthog

Date	*Catena:*	Low	Med.	High	Total
16/09/81		5	10	4	19
20/09/81		4	9	2	15
04/10/81		3	5	2	10
11/10/81		9	10	2	21
27/10/81		11	7	3	21
13/11/81		17	14	5	36
08/12/81		17	37	1	55
13/12/81		30	32	5	67
20/12/82		29	34	12	75
07/01/82		44	46	27	117
12/01/82		29	49	14	88
20/01/82		35	64	4	103
01/02/82		25	106	27	158
07/02/82		6	66	10	82
14/02/82		13	46	24	83
22/02/82		0	29	5	34
01/03/82		14	21	2	27
08/03/82		18	18	3	39
18/03/82		11	27	3	41
24/03/82		2	10	5	17
30/03/82		8	12	6	26
07/04/82		1	37	7	46
13/04/82		7	22	9	38
27/04/82		6	36	0	42
04/05/82		0	37	1	38
10/05/82		0	32	35	67
29/05/82		2	12	0	14
05/06/82		2	35	11	48
10/06/82		0	33	18	51
19/06/82		0	27	26	53
27/06/82		3	10	21	34
09/07/82		0	5	19	24
15/07/82		0	8	2	10
23/07/82		0	8	3	11
29/07/82		4	9	5	18
13/08/82		4	5	0	9
27/08/82		9	11	6	26
02/09/82		24	41	24	89
12/09/82		6	28	8	42
25/09/82		16	66	19	101
03/10/82		5	22	13	40
09/10/82		8	61	0	69

10: Giraffe

Date	*Catena:*	Low	Med.	High	Total
16/09/81		0	9	0	9
20/09/81		0	12	0	12
04/10/81		1	11	0	12
11/10/81		1	3	0	4
27/10/81		0	6	0	6
13/11/81		0	0	0	0
08/12/81		3	0	7	10
13/12/81		0	2	0	2
20/12/82		0	0	0	0
07/01/82		3	2	0	5
12/01/82		0	0	0	0
20/01/82		2	4	0	6
01/02/82		1	0	3	4
07/02/82		0	0	0	0
14/02/82		3	2	0	5
22/02/82		0	11	0	11
01/03/82		0	0	0	0
08/03/82		0	9	0	9
18/03/82		3	2	0	5
24/03/82		0	5	0	5
30/03/82		3	1	0	4
07/04/82		2	1	0	3
13/04/82		0	1	0	1
27/04/82		0	1	0	1
04/05/82		0	0	1	1
10/05/82		0	0	4	4
29/05/82		0	3	2	5
05/06/82		0	2	0	2
10/06/82		0	0	0	0
19/06/82		0	0	0	0
27/06/82		0	0	0	0
09/07/82		0	0	0	0
15/07/82		0	0	0	0
23/07/82		0	0	0	0
29/07/82		0	0	1	1
13/08/82		0	4	0	4
27/08/82		0	0	0	0
02/09/82		4	0	0	4
12/09/82		0	7	0	7
25/09/82		0	19	0	19
03/10/82		0	4	0	4
09/10/82		0	4	1	5

11: Kongoni

Date	*Catena:*	Low	Med.	High	Total
16/09/81		7	1	0	8
20/09/81		1	2	0	3
04/10/81		0	0	0	0
11/10/81		11	0	0	11
27/10/81		0	0	0	0
13/11/81		18	1	0	19
08/12/81		17	0	0	17
13/12/81		7	0	0	7
20/12/82		5	0	0	5
07/01/82		1	8	0	9
12/01/82		1	21	0	22
20/01/82		3	1	1	5
01/02/82		0	0	0	0
07/02/82		17	0	0	17
14/02/82		0	6	0	6
22/02/82		0	27	0	27
01/03/82		0	3	0	3
08/03/82		0	0	0	0
18/03/82		8	8	0	16
24/03/82		0	0	0	0
30/03/82		0	0	0	0
07/04/82		0	1	0	1
13/04/82		0	1	0	1
27/04/82		4	0	0	4
04/05/82		11	2	0	13
10/05/82		0	0	1	1
29/05/82		0	1	1	2
05/06/82		0	0	0	0
10/06/82		0	10	0	10
19/06/82		0	0	11	11
27/06/82		2	3	1	6
09/07/82		11	7	1	19
15/07/82		0	0	0	0
23/07/82		0	11	0	11
29/07/82		0	0	0	0
13/08/82		0	0	0	0
27/08/82		0	0	0	0
02/09/82		0	0	0	0
12/09/82		0	0	0	0
25/09/82		0	1	0	1
03/10/82		0	6	0	6
09/10/82		2	0	0	2

12: Eland

Date	*Catena:*	Low	Med.	High	Total
16/09/81		0	0	0	0
20/09/81		0	0	0	0
04/10/81		0	0	0	0
11/10/81		0	0	0	0
27/10/81		0	0	0	0
13/11/81		0	6	0	6
08/12/81		0	5	0	5
13/12/81		0	2	0	2
20/12/82		0	17	0	17
07/01/82		0	0	0	0
12/01/82		1	0	0	1
20/01/82		0	0	0	0
01/02/82		0	0	0	0
07/02/82		0	0	0	0
14/02/82		0	10	0	10
22/02/82		0	0	0	0
01/03/82		0	0	0	0
08/03/82		0	2	0	2
18/03/82		0	0	0	0
24/03/82		32	0	0	32
30/03/82		0	0	0	0
07/04/82		0	8	0	8
13/04/82		0	66	0	66
27/04/82		0	9	0	9
04/05/82		0	2	0	2
10/05/82		0	0	0	0
29/05/82		0	6	0	6
05/06/82		0	9	0	9
10/06/82		0	0	0	0
19/06/82		17	0	0	17
27/06/82		0	0	0	0
09/07/82		0	0	0	0
15/07/82		0	0	0	0
23/07/82		0	0	0	0
29/07/82		0	0	0	0
13/08/82		0	0	0	0
27/08/82		0	0	0	0
02/09/82		0	0	0	0
12/09/82		0	0	0	0
25/09/82		0	0	0	0
03/10/82		0	0	0	0
09/10/82		0	0	0	0

13: Cattle

Date	*Catena:*	Low	Med.	High	Total
16/09/81		175	0	0	175
20/09/81		0	0	0	0
04/10/81		0	0	0	0
11/10/81		0	0	0	0
27/10/81		0	185	0	185
13/11/81		0	0	0	0
08/12/81		0	0	0	0
13/12/81		0	0	0	0
20/12/82		0	0	0	0
07/01/82		0	0	0	0
12/01/82		0	0	0	0
20/01/82		0	0	230	230
01/02/82		0	0	0	0
07/02/82		112	0	0	112
14/02/82		0	55	0	55
22/02/82		160	125	0	285
01/03/82		75	0	0	75
08/03/82		0	0	0	0
18/03/82		0	0	0	0
24/03/82		91	0	0	91
30/03/82		0	0	0	0
07/04/82		21	0	0	21
13/04/82		25	0	0	25
27/04/82		45	0	0	45
04/05/82		0	0	0	0
10/05/82		0	140	0	140
29/05/82		56	125	0	181
05/06/82		0	0	0	0
10/06/82		35	0	0	35
19/06/82		0	126	0	126
27/06/82		0	150	0	150
09/07/82		27	285	0	312
15/07/82		45	63	0	108
23/07/82		155	95	0	250
29/07/82		29	0	0	29
13/08/82		0	0	0	0
27/08/82		52	0	0	52
02/09/82		215	0	0	215
12/09/82		0	0	0	0
25/09/82		6	272	0	278
03/10/82		0	0	0	0
09/10/82		0	0	0	0

14: Shoats (sheep and goats)

Date	*Catena:*	Low	Med.	High	Total
16/09/81		0	0	0	0
20/09/81		0	0	0	0
04/10/81		0	0	0	0
11/10/81		0	0	0	0
27/10/81		0	0	0	0
13/11/81		0	0	0	0
08/12/81		0	0	0	0
13/12/81		0	0	0	0
20/12/82		0	0	0	0
07/01/82		0	0	0	0
12/01/82		0	0	0	0
20/01/82		0	0	0	0
01/02/82		0	0	0	0
07/02/82		0	0	0	0
14/02/82		0	0	0	0
22/02/82		0	0	0	0
01/03/82		0	0	0	0
08/03/82		0	0	0	0
18/03/82		0	0	0	0
24/03/82		0	0	0	0
30/03/82		0	0	0	0
07/04/82		0	0	0	0
13/04/82		0	0	0	0
27/04/82		0	0	0	0
04/05/82		0	0	0	0
10/05/82		0	0	0	0
29/05/82		0	0	0	0
05/06/82		0	0	0	0
10/06/82		0	0	0	0
19/06/82		87	0	0	87
27/06/82		0	87	0	87
09/07/82		0	160	0	160
15/07/82		0	0	0	0
23/07/82		135	0	0	135
29/07/82		185	0	0	185
13/08/82		155	0	0	155
27/08/82		120	0	0	120
02/09/82		0	0	0	0
12/09/82		0	0	0	0
25/09/82		0	0	0	0
03/10/82		0	0	0	0
09/10/82		0	0	0	0

APPENDIX 5

Masai Questionaire

Fourteen Masai were interviewed concerning local attitudes toward the hippopotamus population within the Mara River. Though this sample size cannot be considered large enough to be representative, some interesting qualitative information was collected.

Masai measured the increase in population size primarily by how many livestock watering sites along the river were occupied by hippopotami. Sites are apparently not relocated upon the occupation by a group of hippopotami, though four cattle were killed (out of an estimated 1500 in the area) by hippopotami along the Mara River during 1981.

Three individuals claimed that hippopotami had killed two humans along the river within the past decade, one in 1974, another in 1982.

Of the fourteen individuals interviewed, 6 felt that hippopotami should be protected by the wildlife authorities, 4 did not have any recommendations, and there was one recommendation for each of the following; 1)Shoot all hippopotami around river crossing sites used by Masai, 2)Shoot all adult male hippopotami around these crossing sites, and 3)Protect both hippopotami from poachers and

Masai from hippopotami.

The questionaire was given only to Masai found along the Mara River within 10 km of the field camp. To the North, at the upper end of the 127 km of river included in censuses, there has been an influx of sedentary farm operations, both of large-scale wheat and maize cultivation, and of vegetable cash crops. These farmers were not interviewed.

Masai questionaire and responses

1) *Number of livestock herded?*

14 herds of cattle, ave. size= 101.
range= 75-165.
3 groups of shoats; 65,65, and 250.

2) *Manyatta (temporary village) location?*

All respondents lived within a 10 km radius of the field camp.

3) *Compared with 5 years ago, the hippo population is:*

A/ about the same..... 0
B/ lower..... 0
C/ slightly higher..... 2
D/ much higher..... 12

4) *What is the most important cause of death among adult hippos?*

A/ man..... 1
B/ lion..... 3
C/ crocodile..... 1
D/ other hippos..... 9
E/ disease..... 0
F/ starvation..... 0

5) *When do most hippo deaths occur?*

A/ dry months..... 4
B/ wet months..... 4
C/ no special time..... 1
D/ don't know..... 5

6) *Why do hippos fight with each other?*

A/ for space..... 6
B/ for food..... 0
C/ for breeding..... 8
D/ to protect calves..... 0

7) *When do most fights occur?*

A/ dry months..... 1
B/ wet months..... 13
C/ no special time..... 0
D/ don't know..... 0

8) *How serious are injuries from fighting?*

A/ not serious..... 4
B/ a few deaths..... 8
C/ many deaths..... 2

9) *What length of grass do hippos prefer?*

A/ short-grass..... 2
B/ medium grass..... 8
C/ long-grass..... 4

10) *Do hippos usually graze in the same place?*

A/ seldom..... 5
B/ sometimes..... 3
C/ always..... 6

11) *Do hippos graze within burned areas?*

A/ no..... 4
B/ shortly after burn.... 8
C/ long after burn..... 2

12) *How do hippos affect other wild animals?*

A/ harm..... 3 (forage competition)
B/ no effect..... 10
C/ help..... 1 (keep grass short)

13) *What effect do hippo have on livestock?*

A/ spoil water..... 0
B/ Improve grazing..... 0
C/ destroy grazing..... 4
D/ No effect..... 10

14) *Are hippo dangerous?*

A/ no..... 1
B/ at night..... 3
C/ only bulls..... 2
D/ cows with calves..... 0
E/ always dangerous..... 7
F/ some are dangerous.... 1

15) *What should the government do to manage hippos?*

A/ nothing.....	4
B/ destroy some.....	3*
C/ protect.....	7
D/ allow hunting.....	0

*Specific recommendations in text.